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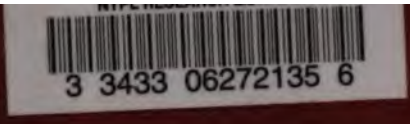
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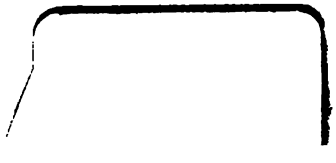

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EDITED BY

E. RAY LANKESTER, M.A., F.R.S., F.L.S.,

Fellow of Exeter College, Oxford, and Professor of Zoology and Comparative Anatomy in University College, London;

WITH THE CO-OPERATION OF

WILLIAM ARCHER, F.R.S., M.R.I.A.,

Dublin.

F. M. BALFOUR, M.A., F.R.S., F.L.S.,

Fellow and Lecturer of Trinity College, Cambridge.

AND

E. KLEIN, M.D., F.R.S.,

Lecturer on Histology in St. Bartholomew's Hospital Medical School, London.

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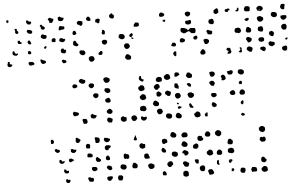

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MEMOIRS.

On the EXISTENCE *of a* HEAD-KIDNEY *in the* EMBRYO CHICK, *and on* CERTAIN POINTS *in the* DEVELOPMENT *of the* MÜLLERIAN DUCT.

By F. M. BALFOUR, M.A., Fellow of Trinity College, Cambridge; and ADAM SEDGWICK, B.A., Scholar of Trinity College, Cambridge. (With Plates I and II).

THE following paper is divided into three sections. The first of these records the existence of certain structures in the embryo chick, which eventually become in part the abdominal opening of the Müllerian duct, and which, we believe, correspond with the head-kidney, or "Vorniere" of German authors. The second deals with the growth and development of the Müllerian duct. With reference to this we have come to the conclusion that the Müllerian duct does not develop entirely independently of the Wolffian duct. The third section of our paper is of a more general character, and contains a discussion of the rectifications in the views of the homologies of the parts of the excretory system in Aves, necessitated by the results of our investigations.

We have, as far as possible, avoided entering into the extended literature of the excretory system, since this has been very fully given in three general papers which have recently appeared by Semper,[1] Fürbringer,[2] and by one of us.[3]

All recent observers, including Braun[4] for Reptilia, and Egli[5] for Mammalia, have stated that the Müllerian duct develops as a groove in the peritoneal epithelium, which is continued backward as a primitively solid rod in the space between the Wolffian duct and peritoneal epithelium.

[1] "Das Urogenital System der Plagiostomen." 'Arbeiten a. d. Zool.-Zoot. Institut. Würzburg.'

[2] "Zur Vergl. Anat. u. Entwick. d. Excretionsorgane d. Vertebraten." 'Morphologisches Jahrbuch,' vol. iv.

[3] "On the Origin and History of the Urino-genital Organs of Vertebrates." 'Journal of Anat. and Phys.,' vol. x.

[4] 'Arbeiten a. d. zool.-zoot. Institut. Würzburg,' vol. iv.

[5] 'Beitr. zur Anat. u. Entwick. d. Geschlechtsorgane,' Inaug. Diss., Zurich, 1876.

In our preliminary account we stated,[1] in accordance with the general view, that the Müllerian duct was formed as a groove, or elongated involution of the peritoneal epithelium adjoining the Wolffian duct. We have now reason to believe that this is not the case. In the earliest condition of the Müllerian duct which we have been able to observe, it consists of three successive open involutions of the peritoneal epithelium, connected together by more or less well-defined ridge-like thickenings of the epithelium. We believe, on grounds hereafter to be stated, that the whole of this formation is equivalent to the head-kidney of the Icthyopsida. The head-kidney, as we shall continue to call it, takes its origin from the layer of thickened epithelium situated near the dorsal angle of the body cavity, close to the Wolffian duct, which has been known since the publication of Waldeyer's important researches as the germinal epithelium. The anterior of the three open involutions or grooves is situated some little distance behind the front end of the Wolffian duct. It is simply a shallow groove in the thickest part of the germinal epithelium, and forms a corresponding projection into the adjacent stroma. In front the projection is separated by a considerable interval from the Wolffian duct; but near its hindermost part it almost comes into contact with the Wolffian duct. The groove extends in all for about five of our sections, and then terminates by its walls becoming gradually continued into a slight ridge-like thickening of the germinal epithelium. The groove arises as a simple depression in a linear area of thickened germinal epithelium. The linear area is, however, continued very considerably further forward than the groove, and sometimes exhibits a slight central depression, which might be regarded as a forward continuation of the groove. The passage from the groove to the ridge may best be conceived by supposing the groove to be suddenly filled up, so as to form a solid ridge pointing inwards towards the Wolffian duct.

The ridge succeeding the first groove is continued for about six sections, and is considerably more prominent at its posterior extremity than in front. It is replaced by groove number two, which appears as if formed by the reverse process to that by which the ridge arose, viz., by a hollowing out of the ridge on the side towards the body cavity. The wall of the second groove is, after a few sections, continued into a second ridge or thickening of the germinal epithelium, which, however, is so faintly marked as to be hardly visible in its middle part. In its turn this ridge is replaced by the third and last groove. This vanishes after one or two sections, and behind the point of its disappearance we have failed to find any further traces of the

[1] 'Proceedings of Royal Society, 1878.'

head-kidney. The whole formation extends through about twenty-four of our sections and one and a half segments (muscle-plates).

We have represented (Plate I, Series A, Nos. 1—10) a fairly complete series of sections through part of the head-kidney of an embryo slightly older than that last described, containing the second and third grooves and accessory parts. The connection between the grooves and the ridges is very well illustrated in Nos. 3, 4, and 5, of this series. In No. 3 we have a prominent ridge, in the interior of which there appears in No. 4 a groove, which becomes gradually wider in Nos. 5 and 6. Both the grooves and ridges are better marked in this than in the younger stage; but the chief difference between the two stages consists in the third groove no longer forming the hindermost limit of the head-kidney. Instead of this, the last groove (No. 7) terminates by the upper part of its walls becoming constricted off as a separate rod, which appears at first to contain a lumen continuous with the open groove. This rod (Nos. 7, 8, 9, 10) situated between the germinal epithelium and Wolffian duct is continued backward for some sections. It finally terminates by a pointed extremity, composed of not more than two cells abreast (Nos. 8—10).

Our third stage, sections of which are represented in series B (Plate I), is considerably advanced beyond that last described. The most important change which has been effected concerns the ridges connecting the successive grooves. A lumen has appeared in each of these, which seems to open at both ends into the adjacent grooves. At the same time the cells, which previously constituted the ridge, have become (except where they are continuous with the walls of the grooves) partially constricted off from the germinal epithelium. The ridges, in fact, now form ducts situated in the stroma of the ovarian ridge, in the space between the Wolffian duct and the germinal epithelium. The duct continuous with the last groove is somewhat longer than before. In a general way, the head-kidney may now be described as a duct opening into the body cavity by three groove-like apertures, and continuous behind with the rudiment of the true Müllerian duct. Although the general constitution of the head-kidney at this stage is fairly simple, there are a few features in our sections which we do not fully understand, and a few points about the organ which deserve a rather fuller description than we have given in this general sketch.

The anterior groove (No. 1—3, series B, Pl. I) is at first somewhat separated from the Wolffian duct, but approaches close to it in No. 3. In Nos. 2 and 3 there appears a rod-like body on the outer side of the walls of the groove. In No. 2

this body is disconnected with the walls of the groove, and even appears as if formed by a second invagination of the germinal epithelium. In No. 3 this body becomes partially continuous with the walls of the groove, and finally in No. 4 it becomes completely continuous with the walls of the groove, and its lumen communicates freely with the groove.[1]

The last trace of this body is seen on the upper wall of the groove in No. 5. We believe that the body (r_1) represents the ridge between the first and second grooves of the earlier stage; so that in passing from No. 3 to No. 5 we pass from the first to the second groove. The meaning of the features of the body r_1 in No. 2 we do not fully understand, but cannot regard them as purely accidental, since we have met with more or less similar features in other series of sections. The second groove becomes gradually narrower, and finally is continued into the second ridge (No. 8). The ridge contains a lumen, and is only connected with the germinal epithelium by a narrow wall of cells. A narrow passage from the body cavity leads into that wall for a short distance in No. 8, but it is probably merely the hinder end of the groove of No 7. The third groove appears in No. 11, and opens into the lumen of the second ridge (r_2) in No. 12. In No. 13 the groove is closed, and there is present in its place a duct (r_3) connected with the germinal epithelium by a wall of cells. This duct is the further development of the third ridge of the last stage; its lumen opens into the body cavity through the third and last groove (gr_3). In the next section this duct (r_3) is entirely separated from the germinal epithelium, and it may be traced backwards through several sections until it terminates by a solid point, very much as in the last stage.

In the figures of this series (B) there may be noticed on the outer side of the Müllerian duct a fold of the germinal epithelium (x) forming a second groove. It is especially conspicuous in the first six sections of the series. This fold sometimes becomes much deeper, and then forms a groove, the upper end of which is close to the grooves of the head-kidney. It is very often much deeper than these are, and without careful study might easily be mistaken for one of these grooves. Fig. C, taken from a series slightly younger than B, shows this groove (x) in its most exaggerated form.

The stage we have just described is that of the fullest development of the head-kidney. In it, as in all the previous stages, there appear to be only three main openings into the body-cavity; but we have met in some of our sections with indications of the possible presence of one or two extra rudimentary grooves.

[1] A deep focus of the rather thick section represented in No. 3 shewed the body much more nearly in the position it occupies in No. 4.

In an embryo not very much older than the one last described the atrophy of the head-kidney is nearly completed, and there is present but a single groove opening into the body cavity.

In series D (Pl. II) are represented a number of sections from an embryo at this stage. Nos. 1 and 2 are sections through the hind end of the single groove now present. Its walls are widely separated from the Wolffian duct in front, but approach close to it at the hinder termination of the groove (No. 2). The features of the single groove present at this stage agree closely with those of the anterior groove of the previous stages. The groove is continued into a duct—the Müllerian duct (as it may now be called, but in a previous stage the hollow ridge connecting the first and second grooves of the head-kidney)—which, after becoming nearly separated from the germinal epithelium, is again connected to it by a mass of cells at two points (Nos. 5, 6, and 8). The germinal epithelium is slightly grooved and is much reduced in thickness at these points of contact (gr_2 and gr_3), and we believe that they are the remnants of the posterior grooves of the head-kidney present at an earlier stage.

The Müllerian duct has by this stage grown much further backwards, but the peculiarities of this part of it are treated in a subsequent section.

We consider that, taking into account the rudiments we have just described, as well as the fact that the features of the single groove at this stage correspond with those of the anterior groove at an earlier stage, we are fully justified in concluding that *the permanent abdominal opening of the Müllerian duct corresponds with the anterior of our three grooves.*

Although we have, on account of their indefiniteness, avoided giving the ages of the chicks in which the successive changes of the head-kidney may be observed, we may, perhaps, state that all the changes we have described are usually completed between the 90th and 120th hour of incubation.

The Glomerulus of the Head-Kidney.

In connection with the head-kidney in Amphibians there is present, as is well known, a peculiar vascular body usually described as the glomerulus of the head-kidney. We have found in the chick a body so completely answering to this glomerulus that we have hardly any hesitation in identifying it as such.

In the chick the glomerulus is paired, and consists of a vascular outgrowth or ridge projecting into the body cavity on each side at the root of the mesentery. It extends from the anterior end of the Wolffian body to the point where the foremost opening of the head-kidney commences. We have found it at a period slightly earlier than that of the first development of the head-

kidney. It is represented in figs. E and F, Pl. II *gl*, and is seen to form a somewhat irregular projection into the body cavity, covered by a continuation of the peritoneal epithelium, and attached by a narrow stalk to the insertion of the embryonic mesentery (*me*).

In the interior of this body is seen a stroma with numerous vascular channels and blood corpuscles, and a vascular connection is apparently becoming established, if it is not so already, between the glomerulus and the aorta. We have reason to think that the corpuscles and vascular channels in the glomerulus are developed *in situ*. The stalk connecting the glomerulus with the attachment of the mesentery varies in thickness in different sections, but we believe that the glomerulus is continued unbroken throughout the very considerable region through which it extends. This point is, however, difficult to make sure of owing to the facility with which the glomerulus breaks away.

At the stage we are describing, no true Malpighian bodies are present in the part of the Wolffian body on the same level with the anterior end of the glomerulus, but the Wolffian body merely consists of the Wolffian duct. At the level of the posterior part of the glomerulus this is no longer the case, but here a regular series of primary Malpighian bodies is present (using the term "primary" to denote the Malpighian bodies developed directly out of part of the primary segmental tubes), and the glomerulus of the head-kidney may frequently be seen in the same section as a Malpighian body. In most sections the two bodies appear quite disconnected, but in those sections in which the *glomerulus* of the Malpighian body comes into view it is seen to be derived from the same formation as the glomerulus of the head-kidney (Plate II, fig. F). It would seem, in fact, that the vascular tissue of the glomerulus of the head-kidney grows into the concavity of the Malpighian bodies. Owing to the stage we are now describing, in which we have found the glomerulus most fully developed, being prior to that in which the head-kidney appears, it is not possible to determine with certainty the position of the glomerulus in relation to the head-kidney. After the development of the head-kidney it is found, however, as we have already stated, that the glomerulus terminates at a point just in front of the anterior opening of the head-kidney. It is less developed than before, but is still present up to the period of the atrophy of the head-kidney. It does not apparently alter in constitution, and we have not thought it worth while giving any further representations of it during the later stages of its existence.

Summary of the development of the head-kidney and glomerulus.—The first rudiment of the head-kidney arises as three successive *grooves* in the thickened germinal epithelium, connected by ridges,

and situated some way behind the front end of the Wolffian duct. In the next stage the three ridges connecting the grooves have become more marked, and in each of them a lumen has appeared, opening at both extremities into the adjoining grooves. Still later the ridges become more or less completely detached from the peritoneal epithelium, and the whole head-kidney then consists of a slightly convoluted duct, with, at the least, three peritoneal openings, which is posteriorly continued into the Müllerian duct. Still later the head-kidney atrophies, its two posterior openings vanishing, and its anterior opening remaining as the permanent opening of the Müllerian duct. The glomerulus arises as a vascular prominence at the root of the mesentery, slightly prior in point of time to the head-kidney, and slightly more forward than it in position. We have not traced its atrophy.

We stated in our preliminary paper that the peculiar structures we had interpreted as the head-kidney had completely escaped the attention of previous observers, though we called attention to a well-known figure of Waldeyer's (copied in the 'Elements of Embryology,' fig. 51). In this figure a connection between the germinal epithelium and the Müllerian duct is drawn, which is probably part of the head-kidney, and may be compared with our figures (Series B, No. 8, and Series D, No. 4). Since we made the above statement, Dr. Gasser has called our attention to a passage in his valuable memoir on 'The Development of the Allantois,'[1] in which certain structures are described which are, perhaps, identical with our head-kidney. The following is a translation of the passage:—

"In the upper region of Müller's duct I have often observed small canals, especially in the later stages of development, which appear as a kind of doubling of the duct, and run for a short distance close to Müller's duct and in the same direction, opening, however, into the body cavity posterior to the main duct. Further, one may often observe diverticula from the extreme anterior end of the oviduct of the bird, which form blind pouches and give one the impression of being receptacula seminis. Both these appearances can quite well be accounted for on the supposition that an abnormal communication is effected between the germinal epithelium and Müller's duct at unusual places; or else that an attempt at such a communication is made, resulting, however, only in the formation of a diverticulum of the wall of the oviduct."

The statement that these accessory canals are late in developing, prevents us from feeling quite confident that they really correspond with our head-kidney.

[1] 'Beiträge zur Entwicklungsgeschichte d. Allantois der Müller'schen Gänge u. des Afters.' Frankfurt, 1874.

Before passing on to the other parts of this paper it is necessary to say a few words in justification of the comparison we have made between the modified abdominal extremity of the Müllerian duct in the chick and the head-kidney of the Icthyopsida.

For the fullest statement of what is known with reference to the anatomy and development of the head-kidney in the lower types we may refer to Spengel and Fürbringer.[1] We propose ourselves merely giving a sufficient account of the head-kidney in Amphibia (which appears to be the type in which the head-kidney can be most advantageously compared with that in the bird) to bring out the grounds for our determination of the homologies.

The development of the head-kidney in Amphibia has been fully elucidated by the researches of W. Müller,[2] Götte,[3] and Fürbringer,[4] while to the latter we are indebted for a knowledge of the development of the Müllerian duct in Amphibians. The first part of the urino-genital system to develop is the segmental duct (Vornieregang of Fürbringer), which is formed by a groove-like invagination of the peritoneal epithelium. It becomes constricted into a duct first of all in the middle, but soon in the posterior part also. It then forms a duct, ending in front by a groove in free communication with the body cavity, and terminating blindly behind. The open groove in front at first deepens, and then becomes partially constricted into a duct, which elongates and becomes convoluted, but remains in communication with the body cavity by from two to four (according to the species) separate openings. The manner in which the primitive single opening is related to the secondary openings is not fully understood. By these changes there is formed out of the primitive groove an anterior glandular body, communicating with the body cavity by several apertures, and a posterior duct, which carries off the secretion of the gland, and which, though blind at first, eventually opens into the cloaca. In addition to these parts there is also formed on each side of the mesentery, opposite the peritoneal openings, a very vascular projection into this part of the body cavity, which is known as the glomerulus of the head-kidney, and which very closely resembles in structure and position the body to which we have assigned the same name in the chick.

The primitive segmental duct is at first only the duct for the head-kidney, but on the formation of the posterior parts of the kidney (Wolffian body, &c.) it becomes the duct for these also.

[1] Loc. cit.
[2] 'Jenaische Zeitschrift,' vol. ix, 1875.
[3] 'Entwickelungsgeschichte d. Unke.'
[4] Loc. cit.

After the Wolffian bodies have attained to a considerable development, the head-kidney undergoes atrophy, and its peritoneal openings become successively closed from before backwards. At this period the formation of the Müllerian duct takes place. It is a solid constriction of the ventral or lateral wall of the segmental duct, which subsequently becomes hollow, and acquires an opening into the body cavity *quite independent of the openings of the head-kidney*.

The similarity in development and structure between the head-kidney in Amphibia and the body we have identified as such in Aves, is to our minds too striking to be denied. Both consist of two parts—(1) a somewhat convoluted longitudinal canal, with a certain number of peritoneal openings; (2) a vascular prominence at the root of the mesentery, which forms a glomerulus. As to the identity in position of the two organs we hope to deal with that more fully in speaking of the general structure of the excretory system, but may say that one of us[1] has already, on other grounds, attempted to show that the abdominal opening of the Müllerian duct in the bird is the homologue of the abdominal opening of the segmental duct in Amphibia, Elasmobranchii, &c., and that we believe that this homology will be admitted by most anatomists. If this homology is admitted, the identity in position of this organ in Aves and Amphibia necessarily follows. The most striking difference between Aves and Amphibia in relation to these structures is the fact that in Aves the anterior pore of the head-kidney remains as the permanent opening of the Müllerian duct, while in Amphibia, the pores of the head-kidney atrophy, and an entirely fresh abdominal opening is formed for the Müllerian duct.

II.

The Growth of the Müllerian Duct.

Although a great variety of views have been expressed by different observers on the growth of the Müllerian duct, it is now fairly generally admitted that it grows in the space between a portion of the thickened germinal epithelium and the Wolffian duct, but quite independently of both of them. Both Braun and Egli, who have specially directed their attention to this point, have for Reptilia and Mammalia fully confirmed the views of previous observers. We were, nevertheless, induced, partly on account of the *à priori* difficulties of this view, and partly by certain peculiar appearances which we observed, to undertake the re-examination of this point, and have found ourselves unable altogether to accept the general account. We propose first

[1] Balfour, "Origin and History of Urinogenital Organs of Vertebrates." 'Journal of Anat. and Phys.,' vol. x, and "Monograph on Elasmobranch Fishes."

describing, in as matter-of-fact a way as possible, the actual observations we have made, and then stating what conclusions we think may be drawn from these observations.

We have found it necessary to distinguish three stages in the growth of the Müllerian duct. Our first stage embraces the period prior to the disappearance of the head-kidney. At this stage the structure we have already spoken of as the rudiment of the Müllerian duct consists of a solid rod of cells, continuous with the third groove of the head-kidney. It extends through a very few sections, and terminates by a fine point of about two cells, wedged in between the Wolffian duct and germinal epithelium (described above, No. 7—10, series A, Plate I).

In an embryo slightly older than the above, such as that from which series B was taken, but still belonging to our first stage, a definite lumen appears in the anterior part of the Müllerian duct, which vanishes after a few sections. The duct terminates in a point which lies in a concavity of the wall of the Wolffian duct (Plate I, Nos. 1 and 2, series G). The limits of the Wolffian wall and the pointed termination of the Müllerian duct are in many instances quite distinct; but the outline of the Wolffian duct appears to be carried round the Müllerian duct, and in some instances the terminal point of the Müllerian duct seems almost to form an integral part of the wall of the Wolffian duct.

The second of our stages corresponds with that in which the atrophy of the head-kidney is nearly complete (series D and H, Plate II).

The Müllerian duct has by this stage made a very marked progress in its growth towards the cloaca, and, in contradistinction to the earlier stage, a lumen is now continued close up to the terminal point of the duct. In the two or three sections before it ends it appears as a distinct oval mass of cells (No. 10, series D, and No. 1, series H), without a lumen, lying between and touching the external wall of the Wolffian duct on the one hand, and the germinal epithelium on the other. It may either lie on the ventral side of the Wolffian duct (series D), or on the outer side (series H), but in either case is opposite the maximum thickening of that part of the germinal epithelium which always accompanies the Müllerian duct in its backward growth.

In the last section in which any trace of the Müllerian duct can be made out (series D, No. 11, and series H, No. 2), it has no longer an oval, well-defined contour, but appears to have completely fused with the wall of the Wolffian duct, which is accordingly very thick, and occupies the space which in the previous section was filled by its own wall and the Müllerian duct. In the following section the thickening in the wall of the

Wolffian duct has disappeared (Plate II, series H, No. 3), and every trace of the Müllerian duct has vanished from view. The Wolffian duct is on one side in contact with the germinal epithelium.

The stage during which the condition above described lasts is not of long duration, but is soon succeeded by our third stage, in which a fresh mode of termination of the Müllerian duct is found. (Plate II, series I). This last stage remains up to about the close of the sixth day, beyond which our investigations do not extend.

A typical series of sections through the terminal part of the Müllerian duct at this stage presents the following features:

A few sections before its termination the Müllerian duct appears as a well-defined oval duct lying in contact with the wall of the Wolffian duct on the one hand and the germinal epithelium on the other (series I, No. 1). Gradually, however, as we pass backwards, the Müllerian duct dilates; the external wall of the Wolffian duct adjoining it becomes greatly thickened and pushed in in its middle part, so as almost to touch the opposite wall of the duct, and so form a bay in which the Müllerian duct lies (Plate II, series I, Nos. 2 and 3). As soon as the Müllerian duct has come to lie in this bay its walls lose their previous distinctness of outline, and the cells composing them assume a curious vacuolated appearance. No well-defined line of separation can any longer be traced between the walls of the Wolffian duct and those of the Müllerian, but between the two is a narrow clear space traversed by an irregular network of fibres, in some of the meshes of which nuclei are present.

The Müllerian duct may be traced in this condition for a considerable number of sections, the peculiar features above described becoming more and more marked as its termination is approached. It continues to dilate and attains a maximum size in the section or so before it disappears. A lumen may be observed in it up to its very end, but is usually irregular in outline and frequently traversed by strands of protoplasm. The Müllerian duct finally terminates quite suddenly (Plate II, series I, No. 4), and in the section immediately behind its termination the Wolffian duct assumes its normal appearance, and the part of its outer wall on the level of the Müllerian duct comes into contact with the germinal epithelium (Plate II, series I, No. 5).

We have traced the growing point of the Müllerian duct with the above features till not far from the cloaca, but we have not followed the last phases of its growth and its final opening into the cloaca.

In some of our embryos we have noticed certain rather peculiar structures, an example of which is represented at *y* in fig. K, taken from an embryo of 123 hours, in which all traces of the head-kidney had disappeared. It consists of a cord of cells, connecting the Wolffian duct and the hind end of the abdominal opening of the Müllerian duct. At the least one similar cord was met with in the same embryo, situated just behind the abdominal opening of the Müllerian duct. We have found similar structures in other embryos of about the same age, though never so well marked as in the embryo from which fig. K is taken. We have quite failed to make out the meaning, if any, of them.

Our interpretation of the appearances we have described in connection with the growth of the Müllerian duct can be stated in a very few words. Our second stage, where the solid point of the Müllerian duct terminates by fusing with the walls of the Wolffian duct, we interpret as meaning that the Müllerian is growing backwards as a solid rod of cells, split off from the outer wall of the Wolffian duct; in the same manner, in fact, as in Amphibia and Elasmobranchii. The condition of the terminal part of the Müllerian duct during our third stage cannot, we think, be interpreted in the same way, but the peculiarities of the cells of both Müllerian and Wolffian ducts, and the indistinctness of the outlines between them, appear to indicate that the Müllerian duct grows by cells passing from the Wolffian duct to it. In fact, although in a certain sense the growth of the two ducts is independent, yet the actual cells which assist in the growth of the Müllerian duct are, we believe, derived from the walls of the Wolffian duct.

III.

General Considerations.

The excretory system of a typical Vertebrate consists of the following parts:—

1. A head-kidney with the characters already described.
2. A duct for the head-kidney—the segmental duct.
3. A posterior kidney—(Wolffian body, permanent kidney, &c. The nature and relation of these parts we leave out of consideration, as they have no bearing upon our present investigations.) The primitive duct for the Wolffian body is the segmental duct.
4. The segmental duct may become split into (*a*) a dorsal or inner duct, which serves as ureter (in the widest sense of the word); and (*b*) a ventral or outer duct, which has an opening into the body cavity, and serves as the generative duct for the female, or for both sexes.

These parts exhibit considerable variations both in their struc-

ture and development, into some of which it is necessary for us to enter.

The head-kidney[1] attains to its highest development in the Marsipobranchii (Myxine, Bdellostoma). It consists of a longitudinal canal, from the ventral side of which numerous tubules pass. These tubules, after considerable subdivision, open by a large number of apertures into the pericardial cavity. From the longitudinal canal a few dorsal diverticula, provided with glomeruli, are given off. In the young the longitudinal canal is continued into the segmental duct; but this connection becomes lost in the adult. The head-kidney remains, however, through life. In Teleostei and Ganoidei (?) the head-kidney is generally believed to remain through life, as the dilated cephalic portion of the kidneys when such is present. In Petromyzon and Amphibia the head-kidney atrophies. In Elasmobranchii the head-kidney, so far as is known, is absent.

The development of the segmental duct and head-kidney (when present)is still more important for our purpose than their adult structure.

In Myxine the development of these structures is not known. In Amphibia and Teleostei it takes place upon the same type, viz., by the conversion of a groove-like invagination of the peritoneal epithelium into a canal open in front. The head-kidney is developed from the anterior end of this canal, the opening of which remains in Teleostei single and closes early in embryonic life, but becomes in Amphibia divided into two, three, or four openings. In Elasmobranchii the development is very different.

"The first trace of the urinary system makes its appearance as a knob springing from the intermediate cell-mass opposite the fifth proto-vertebra. This knob is the rudiment of the abdominal opening of the segmental duct, and from it there grows backwards to the level of the anus a solid column of cells, which constitutes the rudiment of the segmental duct itself. The knob projects towards the epiblast, and the column connected with it lies between the mesoblast and epiblast. The knob and column do not long remain solid, but the former acquires an opening into

[1] I am inclined to give up the view I formerly expressed with reference to the head-kidney and segmental duct, viz. "that they were to be regarded as the most anterior segmental tube, the peritoneal opening of which had become divided, and which had become prolonged backwards so as to serve as the duct for the posterior segmental tubes," and *provisionally* to accept the Gegenbaur-Fürbringer view which has been fully worked out and ably argued for by Fürbringer (loc. cit. p. 96). According to this view the head-kidney and its duct are to be looked on as the primitive and unsegmented part of the excretory system, more or less similar to the excretory system of many Trematodes and unsegmented Vermes. The segmental tubes I regard as a truly segmental part of the excretory system acquired subsequently.—F. M. B.

the body-cavity continuous with a lumen, which makes its appearance in the latter."

The difference in the development of the segmental duct in the two types) Amphibia and Elasmobranchii) is very important. In the one case a continuous groove of the peritoneal epithelium becomes constricted into a canal, in the other a solid knob of cells is continued into a rod, at first solid, which grows backwards without any apparent relation to the peritoneal epithelium

The abdominal aperture of the segmental duct in Elasmobranchii, in that it becomes the permanent abdominal opening of the oviduct, corresponds physiologically rather with the abdominal opening of the Müllerian duct than with that of the segmental duct of Amphibia, which, after becoming divided up to form the pores of the head-kidney, undergoes atrophy. Morphologically, however, it appears to correspond with the opening of the segmental duct in Amphibia. We shall allude to this point more than once again, and give our grounds for the above view on p. 19.

The development of the segmental duct in Elasmobranchii as a solid rod is, we hope to show, of special importance for the elucidation of the excretory system of Aves.

The development of these parts Petromyzon is not fully known, but from W. Müller's account ('Jenaische Zeitschrift,' 1875) it would seem that an anterior invagination of the peritoneal epithelium is continued backwards as a duct (segmental duct), and that the anterior opening subsequently becomes divided up into the various apertures of the head-kidney. If this account

[1] In a note on p. 50 of his memoir Fürbringer criticises my description of the mode of growth of the segmental duct. The following is a free translation of what he says: "In Balfour's, as in other descriptions, an account is given of a backward growth, which easily leads to the supposition of a structure formed anteriorly forcing its way through the tissues behind. This is, however, not the case, since, to my knowledge, no author has ever detected a sharp boundary between the growing point of the segmental duct (or Müllerian duct) and the surrounding tissues." He goes on to say that "the growth in these cases really takes place by a differentiation of tissue along a line in the region of the peritoneal cavity." Although I fully admit that it would be far easier to homologise the development of the segmental duct in Amphibia and Elasmobranchii according to this view, I must nevertheless vindicate the accuracy of my original account. I have looked over my specimens again, since the appearance of Dr. Fürbringer's paper, and can find no evidence of the end of the duct becoming continuous with the adjoining mesoblastic tissues. In the section, before its disappearance, the segmental duct may, so far as I can make out, be seen as a very small but distinct rod, which is much more closely connected with the epiblast than with any other layer. From Gasser's observations on the Wolffian duct in the bird, I am led to conclude that it behaves in the same way as the segmental duct in the Elasmobranchii. I will not deny that it is possible that the growth of the duct takes place by wandering cells, but on this point I have no evidence, and must therefore leave the question an open one.—F. M. B.

is correct, Petromyzon presents a type intermediate between Amphibia and Elasmobranchii. In certain types, viz., Marsipobranchii and Teleostei, the segmental duct becomes the duct for the posterior kidney (segmental tubes), but otherwise undergoes no further differentiation. In the majority of types, however, the case is different. In Amphibia,[1] as has already been mentioned, a solid rod of cells is split off from its ventral wall, which afterwards becomes hollow, acquires an opening into the body cavity, and forms the Müllerian duct.

In Elasmobranchii the segmental duct undergoes a more or less similar division. "It becomes longitudinally split into two complete ducts in the female, and one complete duct and parts of a second in the male. The resulting ducts are the (1) Wolffian duct dorsally, which remains continuous with the excretory tubules of the kidney, and ventrally (2) the oviduct or Müllerian duct in the female, and the rudiments of this duct in the male. In the female the formation of these ducts takes place by a nearly solid rod of cells, being gradually split off from the ventral side of all but the foremost part of the original segmental duct, with the short undivided anterior part of which duct it is continuous in front. Into it a very small portion of the lumen of the original segmental duct is perhaps continued. The remainder of the segmental duct (after the loss of its anterior section and the part split off from its ventral side) forms the Wolffian duct The process of formation of the ducts in the male chiefly differs from that in the female, in the fact of the anterior undivided part of the segmental duct, which forms the front end of the Müllerian duct, being shorter, and in the column of cells with which it is continuous being from the first incomplete."

It will be seen from the above that the Müllerian duct consists of two distinct parts—an anterior part with the abdominal opening, and a posterior part split off from the segmental duct. This double constitution of the Müllerian duct is of great importance for a proper understanding of what takes place in the Bird.

The Müllerian duct appears therefore to develop in nearly the same manner in the Amphibian and Elasmobranch type, as a solid or nearly solid rod split off from the ventral wall of the segmental duct. But there is one important difference concerning the abdominal opening of the duct. In Amphibia this is a new formation, but in Elasmobranchii it is the original opening of the segmental duct. Although we admit that in a large number of points, including the presence of a head-kidney, the urino-genital organs of Amphibia are formed on a lower type than those of the Elasmobranchii, yet it appears to us that this does not hold good for the development of the Müllerian duct.

[1] Fürbringer, loc. cit.

The above description will, we trust, be sufficient to render clear our views upon the development of the excretory system in Aves.

In the bird the excretory system consists of the following parts (using the ordinary nomenclature) which are developed in the order below.

1. Wolffian duct. 2. Wolffian body. 3. Head-kidney. 4. Müllerian duct. 5. Permanent kidney and ureter.

About 2 and 5 we shall have nothing to say in the sequel.

We have already in the early part of the paper given an account of the head-kidney and Müllerian duct, but it will be necessary for us to say a few words about the development of the Wolffian duct (so called). Without entering into the somewhat extended literature on the subject, we may state that we consider that the recent paper of Dr. Gasser[1] supplies us with the best extant account of the development of the Wolffian duct.

The first trace of it, which he finds, is visible in an embryo with eight proto-vertebræ as a slight projection from the intermediate cell mass towards the epiblast in the region of the three hindermost proto-vertebræ. In the next stage, with eleven proto-vertebræ, the solid rudiment of the duct extends from the fifth to the eleventh proto-vertebra, from the eighth to the eleventh proto-vertebra it lies between the epiblast and mesoblast, and is quite distinct from both, and Dr. Gasser distinctly states that in its growth backwards from the eighth proto-vertebra the Wolffian duct never comes into continuity with the adjacent layers.

In the region of the fifth proto-vertebra, where the duct was originally continuous with the mesoblast, it has now become free, but is still attached in the region of the sixth and to the eighth proto-vertebra. In an embryo with fourteen proto-vertebræ the duct extends from the fourth to the fourteenth proto-vertebra, and is now free between epiblast and mesoblast for its whole extent. It is still for the most part solid though perhaps a small lumen is present in its middle part. In the succeeding stages the lumen of the duct gradually extends backwards and forwards, the duct itself also passes inwards till it acquires its final position close to the peritoneal epithelium; at the same time its hind end elongates till it comes into connection with the cloacal section of the hind-gut. It should be noted that the duct in its backward growth does not appear to come into continuity with the subjacent mesoblast, but behaves in this respect exactly as does the segmental duct in Elasmobranchii (*vide* note on p. 14).

The question which we propose to ourselves is the following:—What are the homologies of the parts of the Avian urinogenital system above enumerated? The Wolffian duct appears to us mor-

[1] 'Arch. für Mic. Anat.,' vol. xiv.

phologically to correspond *in part* to the segmental duct,[1] or what Fürbringer would call the duct of the head-kidney. This may seem a paradox, since in birds it never comes into relation with the head-kidney. Nevertheless we consider that this homology is morphologically established, for the following reasons :—

(1) That the Wolffian duct gives rise (*vide supra*, p. 12) to the Müllerian duct as well as to the duct of the Wolffian body. In this respect it behaves precisely as does the segmental duct of Elasmobranchii and Amphibia. That it serves as the duct for the Wolffian body, before the Müllerian duct originates from it, is also in accordance with what takes place in other types.

(2) That it develops in a strikingly similar manner to the segmental duct of Elasmobranchii.

We stated expressly that the Wolffian duct corresponded only in part to the segmental duct. It does not, in fact, in our opinion, correspond to the whole segmental duct, but to the segmental duct minus the anterior abdominal opening in Elasmobranchii, which becomes the head-kidney in other types. In fact, we suppose that the segmental duct and head-kidney, which in the Ichthyopsida develop as a single formation, develop in the Bird as two distinct structures—one of these known as the Wolffian duct, and the other the head-kidney. If our view about the head-kidney is accepted the above position will hardly require to be disputed, but we may point out that the only feature in which the Wolffian duct of the Bird differs in development from the segmental duct of Elasmobranchii is in the absence of the knob, which forms the commencement of the segmental duct, and in which the abdominal opening is formed ; so that the comparison of the development of the duct in the two types confirms the view arrived at from other considerations.

The head-kidney and Müllerian duct in the Bird must be considered together. The parts which they eventually give rise to after the atrophy of the head-kidney have almost universally been regarded as equivalent to the Müllerian duct of the Ichthyopsida. By Braun,[2] however, who from his researches on the Lizard satisfied himself of the entire independence of the Müllerian and Wolffian ducts in the Amniota, the Müllerian duct of these forms is regarded as a completely new structure with no genetic relations to

[1] The views here expressed about the Wolffian duct are nearly though not exactly those which one of us previously put forward ('Urinogenital Organs of Vertebrates,' &c., p. 45-46), and with which Fürbinger appears exactly to agree. Possibly Dr. Fürbinger would alter his view on this point were he to accept the facts we believe ourselves to have discovered. Semper's view also differs from ours, in that he believes the Wolffian duct to correspond in its entirety with the segmental duct.

[2] "Urogenital System d. Reptilien." 'Arb. aus d. zool.-zoot. Inst.' Würzburg, vol. iv.

the Müllerian duct of the Ichthyopsida. Semper[1], on the other hand, though he accepts the homology of the Müllerian duct in the Ichthyopsida and Amniota, is of opinion that the anterior part of the Müllerian duct in the Amniota is really derived from the Wolffian duct, though he apparently admits the independent growth of the posterior part of the Müllerian duct. We have been led by our observations, as well as by our theoretical deductions, to adopt a view exactly the reverse of that of Professor Semper. We believe that the anterior part of the Müllerian duct of Aves, which is at first the head-kidney, and subsequently becomes the abdominal opening of the duct, is developed from the peritoneal epithelium independently of all other parts of the excretory system; but that the posterior part of the duct is more or less completely derived from the walls of the Wolffian duct. This view is clearly in accordance with our account of the facts of development in Aves, and it fits in very well with the development of the Müllerian duct in Elasmobranchii. We have already pointed out that in Elasmobranchii the Müllerian duct is formed of two factors—(1) of the whole anterior extremity of the segmental duct, including its abdominal opening; (2) of a rod split off from the ventral side of the segmental duct. In Birds the anterior part (corresponding to factor No. 1) of the Müllerian duct has a different origin from the remainder; so that if the development of the posterior part of the duct (factor No. 2) were to proceed in the same manner in Birds and Elasmobranchii, it ought to be formed at the expense of the Wolffian (*i. e.* segmental) duct, though in connection anteriorly with the head-kidney. And this is what actually appears to take placo.

So far the homologies of the avian excretory system are fairly clear; but there are still some points which have to be dealt with in connection with the permanent opening of the Müllerian duct, and the relatively posterior position of the head-kidney. With reference to the first of these points the facts of the case are the following:—

In Amphibia the permanent opening of the Müllerian duct is formed as an independent opening after the atrophy of the head-kidney.

In Elasmobranchii the original opening of the segmental duct forms the permanent opening of the Müllerian duct and no head-kidney appears to be formed.

In Birds the anterior of the three openings of the head-kidney remains as the permanent opening of the Müllerian duct.

With reference to the difficulties involved in there being apparently three different modes in which the permanent opening

[1] Loc. cit.

of the Müllerian duct is formed, we would suggest the following considerations:

The history of the development of the excretory system teaches us that primitively the segmental duct must have served as efferent duct both for the generative products and kidney secretion (just as the Wolffian duct still does for the testicular products and secretion of the Wolffian body in Elasmobranchii and Amphibia); and further, that at first the generative products entered the segmental duct from the abdominal cavity by one or more of the abdominal openings of the kidney (almost certainly of the head-kidney). That the generative products did not enter the segmental duct at first by an opening specially developed for them appears to us to follow from Dohrn's principle of the transmutation of function (Functionswechsel). As a consequence (by a process of natural selection) of the segmental duct having both a generative and a urinary function, a further differentiation took place, by which that duct became split into two—a ventral Müllerian duct and dorsal Wolffian duct.

The Müllerian duct without doubt was continuous with the head-kidney, and so with the abdominal opening or openings of the head-kidney which served as generative pores. At first the segmental duct was probably split longitudinally into two equal portions, but the generative function of the Müllerian duct gradually impressed itself more and more upon the embryonic development, so that, in the course of time, the Müllerian duct developed less and less at the expense of the Wolffian duct. This process appears partly to have taken place in Elasmobranchii, and still more in Amphibia; the Amphibia offering in this respect a less primitive condition than Elasmobranchii; while in Aves it has been carried even further. The abdominal opening no doubt also became specialised. At first it is quite possible that more than one abdominal pore may have served for the generative products; one of which, no doubt, eventually came to function alone. In Amphibia the specialisation of the opening appears to have gone so far that it no longer has any relation to the head-kidney, and even develops after the atrophy of the head-kidney. In Elasmobranchii, on the other hand, the functional opening appears at a period when we should expect the head-kidney to develop. This state is very possibly the result of a differentiation (along a different line to that in Amphibia) by which the head-kidney gradually ceased to become developed, but by which the primitive opening (which in the development of the head-kidney used to be divided into several pores leading into the body cavity) remained undivided and served as the abdominal aperture of the Müllerian duct. Aves, finally, appear to have become differentiated along a third line;

since in their ancestors the anterior pore of the head-kidney appears to have become specialised as the permanent opening of the Müllerian duct.

With reference to the posterior position of the head-kidney in Aves we have only to remark, that a change in position of the head-kidney might easily take place after it acquired an independent development. The fact that it is slightly behind the glomerulus would seem to indicate, on the one hand, that it has already ceased to be of any functional importance; and, on the other, that the shifting has been due to its having a connection with the Müllerian duct.

We have made a few observations on the development of the Müllerian duct in *Lacerta muralis*, which have unfortunately led us to no decided conclusions. In a fairly young stage in the development of the Müllerian duct (the youngest we have met with), no trace of a head-kidney could be observed, but the character of the abdominal opening of the Müllerian duct was very similar to that figured by Braun.[1] As to the backward growth of the Müllerian duct, we can only state that the solid point of the duct in the young stages is in contact with the wall of the Wolffian duct, and the relation between the two is rather like that figured by Fürbinger (Pl. I, figs. 14-15) in Amphibia.

NOTES *on some of the* RETICULARIAN RHIZOPODA *of the* "CHALLENGER" EXPEDITION. By HENRY B. BRADY, F.R.S. With Plates III, IV, V.

I.—*On new or little known Arenaceous types.*

THE quantity of material, obtained by dredge and tow-net, brought home by the scientific staff of the "Challenger" Expedition is so vast, and the conditions under which it was collected are so varied, that much time must elapse before any detailed account of the results of its examination can be made public. So far as the microzoa are concerned the mere washing, sorting, and examining under the microscope of so large a number of samples of the sea-bottom, to say nothing of the surface-gatherings, has been a long and tedious process; but the time required for their complete investigation and for the preparation of the plates necessary for the illustration of each group of organisms is likely to be an even more considerable source of delay. To no section of the work does this apply

[1] Loc. cit.

with greater force than to the Rhizopoda, and it seems desirable, therefore, that some of the more interesting facts and inferences which have been already acquired should be made the subject of a preliminary notice.

I propose in the present, and perhaps in one or two subsequent papers, to give a brief, and in some respects a provisional description of certain new or little understood types of Rhizopoda, indicating the lines in which additions to our knowledge of the group are furnished by the "Challenger" collections, rather than to attempt anything in the way of systematic history, which can only be rightly done when the results come to be treated collectively and in detail. I shall confine myself to the consideration of types actually obtained in this Expedition, except in one or two instances in which specimens from other sources seem to supply missing links, or otherwise assist in the elucidation of morphological peculiarities.

The list of observing stations drawn up and printed for the use of those engaged in working out the natural history of the Expedition extends to 354 localities. Some of these are represented by mere soundings, of which only a small reference sample of the bottom was preserved, whilst a few include several dredgings made on the same or successive days within a restricted area. Not unfrequently a number of consecutive dredgings in mid-ocean at similar depths are practically identical in their organic constituents, and again, the physical characters of a certain number of the samples are not sufficiently promising to warrant the expenditure of much time over them, so that it has been necessary to make a selection from the series. About fifty dredgings, representing conditions as diverse as possible, were taken in the first place for complete examination, and by the light of the results obtained from these, further selections were made from time to time, until altogether about 140 have been exhaustively worked out. By "exhaustively" I mean that the sand or mud was washed, to begin with, on a sieve of the finest wire gauze (that known as No. 120), the meshes of which were something less than $\frac{1}{120}$th of an inch in diameter. Practically it was found that what passed through this sieve was for the most part veritable mud, composed either of fine inorganic particles, or of the impalpable débris of calcareous tests of one sort or other. Cocoliths were usually present in this finest material, occasionally also the frustules of *Diatomaceæ*, and more commonly the siliceous skeletons of the minute species of *Radiolaria*, but for the Reticularian Rhizopoda it was of little value; not because it did not

contain numberless specimens, but because they belonged invariably to species represented plentifully in the coarser siftings. When there was anything to be gained by doing so it was examined either in water or dry, and balsam mountings were made from it. The material thus washed was sorted by successive siftings, and worked over little by little under a power of about twenty diameters. It is not with the very minute forms that we are concerned in the present paper, but rather with some of the larger types, particularly those which build for themselves composite tests, consisting of sand or other foreign bodies, more or less embedded in calcareous cement or adherent to a chitinous envelope.

Until comparatively recent years but little was known of the larger arenaceous Rhizopoda. The discovery of *Astrorhiza limicola* by Sandahl in 1857 remained unnoticed until attention was drawn to it by the late M. Sars, and before that time probably *Lituola Soldanii* was the largest known living member of the group, whilst amongst fossils the Cretaceous *Lituola* (*Haplophragmium*) *irregulare* held a similar position.

In 1867 the elder Sars discovered *Rhabdammina* and *Saccammina* in deep water off the coast of Norway, and though neither of them were described or figured in his memoir,[1] the kindness of his son, Professor G. O. Sars, in distributing specimens, has left no difficulty as to their identification. The cruise of the "Lightning" in 1868 and of the "Porcupine" in 1869 and the succeeding years, brought to light a considerable series of types not previously known. Some account of these may be found in Dr. Carpenter's 'Microscope and its Revelations' (fifth ed., pp. 530—538), and in a pamphlet[2] prepared for a soirée of the Royal Microscopical Society of London by the same author, and again in a short paper on the Genus *Astrorhiza*,[3] published some time ago in this Journal. The most prominent of the new genera so described are *Pilulina* and *Botellina*, together with a fusiform type assigned to Williamson's genus *Proteonina*,[4] and a "Nautiloid *Lituola*," since named by myself *Cyclammina*. In

[1] "Fortsatte Bemærkninger over det dyriske Livs Udbredning i Havets Dybder," 'Vidensk.-Selsk. Forhandlinger,' for 1868.

[2] 'Descriptive Catalogue of Objects from Deep-sea Dredgings, exhibited at the Soirée of the Royal Microscopical Society, King's College, April 20th, 1870, by Dr. Carpenter, F.R.S., &c.'

[3] "On the Genus Astrorhiza of Sandahl, lately described as Haeckelina by Dr. Bessels," by W. B. Carpenter, M.D., C.B., F.R.S., 'Quart. Journ. Mic. Sci.,' N. S., vol. xvi, pp. 221—224, pl. xix.

[4] Since separated from that genus on good grounds by the Rev. A. M. Norman, who has given it the name of *Marsipella*.

his work on the Microscope, before alluded to, Dr. Carpenter describes and figures many other forms under such names as "Orbuline Lituola," "Globigerine Lituola," "Orthocerine Lituola," and the like. It is much to be regretted that many of these which represent important genera, have never been adequately illustrated, so that they are but little known, except to the few who possess verified specimens. Some of them might very properly have been treated in the present paper, for with one or two exceptions they all have been found in the "Challenger" material, but the limited space available for figures is already crowded with forms for the most part even less known than they are. After all, it is only a few out of a large number of new species that can be alluded to in a brief notice of this sort, and the object has been to select salient types, and leave the intermediate forms for the more extended memoir which will be furnished in the official account of the "Challenger" cruise.

The 'Introduction to the Study of the Foraminifera,' by Dr. Carpenter and Messrs. Parker and Rupert Jones, may be accepted as the epitome of our knowledge of the Order, so far at least as it depends on the minute structure of their tests, at the time of its publication in 1862. In this work the arenaceous types constitute the family LITUOLIDA, and are distributed under three generic heads—*Lituola*, *Trochammina*, and *Valvulina*. *Lituola* is characterised as having a test rough and sandy on the exterior, the interior of the chambers being either simple and undivided or labyrinthic. *Trochammina* is distinguished by the finer materials selected for the construction of the test and the larger proportion of calcareous or ferruginous cement used in their incorporation. The shell-structure in *Valvulina* is described as more open to variation, usually rough and sandy as to its exterior, but sometimes revealing a perforate, calcareous, shelly basis beneath, and the triserial arrangement of the chambers is accepted as the most noteworthy character of the genus.

Professor Reuss, writing about the same time, whilst admitting the difficulties of the position, proposes to divide the somewhat unwieldy group included in the genus *Lituola* of English systematists; and, as a matter of convenience, there was even then, no doubt, much to be said in favour of his view. In his latest work,[1] published after his death, he divides the family LITUOLIDEA of his classification, which is scarcely coextensive with the genus *Lituola* of the "Introduction," into four genera—*Polyphragma*, *Haplophragmium*,

[1] 'Das Elbthalgebirge in Sachsen,' 2ter Theil, p. 119, 1874.

Lituola (proper), and *Haplostiche*. These will be considered at a later stage when the Lituoline forms are spoken of more in detail. It will, however, become manifest as we proceed that neither of these schemes are any longer applicable to the purpose for which they were devised, and the more recent suggestions of Prof. Zittel[1] and Prof. T. Rupert Jones[2] scarcely satisfy the exigencies of the present position. How far the characters on which these and other previous classifications are based, may be of service for the rearrangement of the group, with its enlarged boundaries, will be determined as we go on.

It is not altogether satisfactory to have to depend solely upon the structure and conformation of the external skeleton or test for distinctive characters. There can scarcely be a doubt that the sarcode bodies of animals varying so much in their external features must have important differences. The researches of R. Hertwig, on the animal of *Miliola* and *Rotalia*,[3] and those of F. E. Schulze[4] on *Polystomella* and *Lagena*, permit no longer the belief that the Reticularian Rhizopoda consist of mere masses of undifferentiated protoplasm, and a wide field of investigation is thereby opened, in which the employment of chemical reagents, in conjunction with the higher powers of the microscope, may be expected to yield a harvest of hitherto unnoted facts. But, for these methods of research the fresh, if not the living animals, can alone be used; material long preserved in alcohol, as the "Challenger" dredgings have necessarily been, furnishes only the knowledge derivable from the harder tissues and the portions rendered permanent by inorganic constituents.

There is one question to which attention must for a moment be directed before entering upon more strictly morphological considerations, namely, the chemical composition of these arenaceous tests. It is not often that specimens of any single species of recent Foraminifera can be obtained in sufficient quantity for reliable analysis, but amongst a few of the larger arenaceous forms this can occasionally be done. The dredged material from the "Challenger" Station No. 122 (off Pernambuco), contains *Hyperammina elongata* in considerable abundance, and in No. 24 (off Culebra Island, West Indies) *Cyclammina cancellata*, is one of the most prominent Rhizopods. No better examples than

[1] 'Handbuch der Paläontologie,' 1 Band, 1 Lieferung, 1876.

[2] 'Monthly Micro. Journ.' (Feb., 1876), No. 86, p. 89.

[3] "Bemerkungen zur Organisation und systematischen Stellung der Foraminiferen," 'Jenaische Zeitschr. für Naturwiss.,' vol. x, p. 42, pl. 2, 1876.

[4] 'Archiv für mikr. Anat.,' vol. xiii, 1876.

these could have been chosen for chemical investigation, for the one represents a very sandy non-labyrinthic type, usually but little coloured, the other a finely cemented form with smooth exterior, having its chamber-cavities filled with cancellated shelly growths of deep brown colour. Both species are of considerable size, and about a gramme by weight of each was with some little trouble collected for analysis. I have had the advantage of the assistance of my friend Mr. J. T. Dunn, B. Sc., Demonstrator in the Chemical Laboratory of the College of Physical Science in Newcastle, in this portion of my work.

The specimens were thoroughly washed, in the first place, to free them from soluble saline matter, after which the analysis of *Hyperammina elongata*, gave the following result:

Loss on ignition (organic matter and CO_2)	2·9
Silica	92·5
Peroxide of iron with a little alumina	2·0
Lime and magnesia	2·2
	99·6

Treated in the same way the tests of *Cyclammina cancellata* yielded as follows:

Loss on ignition (organic matter and CO_2)	7·4
Silica	80·5
Peroxide of iron with a little alumina	8·9
Lime	2·9
	99·7

Perhaps the most noteworthy fact conveyed by these figures is the large proportion of ferric oxide the tests of both species, but especially of *Cyclammina*, contain. The iron is present as peroxide, not as silicate or phosphate, and the red colour of the shells is retained or even brightened after ignition. *Hyperammina* gave no phosphoric reaction whatever, and in *Cyclammina* the trace of phosphates was inappreciable. It has been a matter of debate what the red-brown tint of the tests of the arenaceous Rhizopoda is determined by, but so far as these two species are concerned there can be no longer any doubt. At the same time it must not be regarded as proved that iron invariably furnishes the colouring matter of the investment of Foraminifera. I am at present inclined to believe with Dr. Wallich that, in some thin-shelled, calcareous and chitinous forms at least, the brown stain is of organic origin.

The precise way in which the siliceous sand-grains are held together and the nature of the cement, if there be any true inorganic cement, are points not easy to determine; different genera probably differ widely in these particulars. The very small percentage of calcareous matter in proportion to the silica, in both of the above analyses, is a remarkable fact, and one that scarcely accords with the idea that the siliceous material is incorporated by carbonate of lime, as generally set forth.

The smooth tests of the various species of *Trochammina* have been supposed to contain the largest amount of calcareous matter in proportion to siliceous or other embedded constituents of any of the arenaceous Foraminifera; but at great depths, for example at 3000 to 4000 fathoms in the North Pacific, specimens of *Trochammina* (*Ammodiscus*) *incerta* are found, the most delicate of which will bear treatment with nitric acid without material change. Nor is this an isolated fact. I have before me some specimens of *Lituola* (*Reophax*) *nodulosa*, obtained near the Antarctic Circle (Station 156,—1975 fathoms), of large size, that is to say, ranging from half an inch to an inch or even more in length, and stout in proportion. One of these has been digested for a considerable time in nitric acid with the assistance of heat, until everything soluble was removed, yet it still retains its form unimpaired, and has sufficient solidity to bear handling; indeed, the only change apparent to the naked eye is the alteration of colour from dark brown to dirty white. It is clear that in this case the cement was neither calcareous nor ferruginous. In a later paper I shall be able to show that, under certain conditions, true *Miliolæ* are to be met with in which the test is thin, homogeneous, and purely siliceous—so completely siliceous that no effervescence can be detected when the shells are placed in acid under the microscope. It was long since demonstrated that the tests of *Trochamminæ*, living in brackish water, are non-calcareous, though they retain to a great extent their normal sandy exterior, and that one of the *Miliolæ* under similar conditions has a thin, brown, sandy investment. In both these cases the sand-grains are embedded in a chitinous envelope and do not depend on any mineral cement. From such facts it becomes evident that carbonate of lime and peroxide of iron, though secreted to a greater or less extent by many arenaceous Rhizopods, are by no means necessarily the cementing material;—that a chitinous envelope or external layer of altered protoplasm may be the basis to which the sand-grains are adherent or in which they are more or less embedded;—

and lastly, as it can be shown that Foraminifera have the power of secreting silica even to the extent of forming a continuous shelly investment, the easiest explanation of the fact that so many composite tests are not disintegrated by the action of acids, lies in the supposition that secreted silica enters more or less into their composition. At the same time it is quite clear that the precise nature of the investment of many normally arenaceous types is a matter depending largely on external or accidental circumstances.

The fuller consideration of these and kindred matters will arise naturally in the description of the organisms in which they form characteristic features, so that without further preface we may proceed to a review of the more interesting forms belonging to this particular group of Rhizopods.

PSAMMOSPHÆRA FUSCA, *F. E. Schulze*. Pl. IV, figs. 1, 2.

Psammosphæra fusca, F. E. Schulze, 1874. II. Jahresberichte d. Komm. Untersuch. d. deutsch. Meere in Kiel, p. 113, pl. ii, fig. 8, *a—f*.

This is one of the simplest of the arenaceous Foraminifera, and although small specimens are not uncommon in deep water, it remained undescribed until the publication of Professor Schulze's memoir in the North Sea researches above quoted. Ten or twelve years ago I found it in considerable abundance in one of the "Bulldog" soundings obtained by Dr. Wallich, but the specimens were all very small, and it was then difficult to decide whether they were Foraminifera or not. It has been the custom to consider that the tests of the arenaceous Rhizopoda are of necessity imperforate; in other words, that except the single conspicuous pseudopodial orifice the investment is non-porous, and the fact of these specimens having no general aperture seemed to throw doubt upon their nature. But it is now evident that the term "imperforate" is only applicable to a limited number of genera, and that some at least of the sandy forms have more or less porous tests, though, owing to the irregularities of the surface and their rough texture, the orifices are traced with difficulty.

Schulze's description of the species is quite accurate as applied to large specimens. They are spheroidal bodies, from two to four millim. ($\frac{1}{12}$ to $\frac{1}{6}$ inch) in diameter, without any perforations visible to the naked eye, commonly free, but occasionally adherent to small stones. The test itself is from ·25 to ·5 millim. thick, and is composed of coarse sand-grains, united by a cement of fine texture and of characteristic grey-brown colour. Whilst the exterior is more or less rough, owing to

projecting sand-grains or fragments of stone, the interior is throughout even and smooth.

The tendency of the animal to attach itself to foreign bodies is revealed in many different ways; sometimes a fragment but little smaller than the remainder of the test, is built into the wall; in other cases the shell is erected, tent-like, upon a stone. In one of the "Challenger" dredgings (Station 122—350 fathoms, off the coast of Brazil) minute specimens are very common, and in a large proportion of them the test is built upon or around a sponge-spicule. One of these, with the side partially ground to show the interior, is represented in Pl. II, fig. 2.

It is somewhat remarkable that, notwithstanding the thickness of the test and its rough composite texture, these sandy spheres are quite translucent when fresh, and they retain their character for a long period if preserved in glycerine or diluted alcohol.

The specimens described by Professor Schulze were found in mud, from depths of 100 to 200 fathoms, in the North Sea, but the species is of not unfrequent occurrence in the "Challenger" material from stations both in the North and South Atlantic and in the North Pacific, at depths varying from 250 to 2740 fathoms, In the deeper dredgings the examples are invariably small.

Psammosphæra fusca may also be added to the list of British species, as it occurs in sands dredged in Loch Scavaig (Skye) from 45 to 60 fathoms.

Genus—SOROSPHÆRA, *nov.*

(σωρός, heap; σφαῖρα, a sphere.)

SOROSPHÆRA CONFUSA, *n.sp.* Pl. IV, figs. 18, 19.

Characters.—Test free, irregular; consisting of a number of convex or sphæroidal chambers, either discrete or more or less embracing, irregularly crowded together. Walls thin, loosely arenaceous in texture. General aperture, none. Long diameter of large specimens, $\frac{1}{6}$ inch (4·5 millim.).

There is, so far as I am aware, no recognised genus in which the large irregular polythalamous Rhizopods, with characters somewhat roughly indicated in the foregoing description, can be properly placed. One of their most striking features is the absence of any general aperture. In none of the specimens I have met with can any definite general pseudopodial orifice be detected. One or two of them have a sort of crack or fissure in the depression between two of

the segments, but it appears to be the result of accident, and the specimens are not otherwise complete. If this be the normal condition of the test, and it may be assumed that it is, it would suggest a near affinity to the genus *Psammosphæra*. That the comparatively thick and well-cemented test of *Psammosphæra* affords free passage for the sarcode in the form of pseudopodia, without any general aperture, is a well-ascertained fact, and there can be no difficulty, therefore, in supposing that *Sorosphæra* with its thinner shell of open granular texture does the same; in point of fact, these two genera are in very similar position to some of the hyaline calcareous Foraminifera, such as *Orbulina*, which depend on minute foramina rather than on a large central orifice for the means of extending their sarcode beyond the limits of the chamber-cavities. I have long been convinced that the use of the words "Perforate" and "Imperforate," as a class distinction amongst the Foraminifera, is an untenable one, and these types are sufficient evidence that the arenaceous forms at any rate are not necessarily imperforate.

In some genera of Foraminifera, *Cristellaria*, for example, specimens may be found in which the stoloniferous tubes uniting the chamber-cavities are distinct from the radiate orifices that have in succession served as the general aperture; but such case are rare and, as a rule, the general aperture of the terminal chamber forms the passage connecting it with the cavity of the segment next formed. It follows, therefore, that in a polythalamous test like *Sorosphæra*, in which there is no external general aperture, the sarcode segments cannot be connected by stolons, and unless the pores of the contiguous chamber-walls serve the purpose of stoloniferous passages, the individual chambers must have a separate rather than a corporate existence. We know, however that the sarcode of perforate Foraminifera spreads itself freely over the surface of the shell before extending itself in pseudopodial filaments, and there can be little doubt that the interstices amongst the sand-grains of the contiguous chamber-walls are sufficient to afford free communication between the segments.

The absence of any general aperture may be held to account for the irregular growth of the test and the want of order amongst the segments, for it is clear that if the protoplasm exudes at all points of the surface, a fresh chamber may be formed whenever sufficient has collected at one spot to segregate itself into a mass of the requisite size.

The specimen figured (Pl. IV, fig. 18) is the largest, and on the whole the best, that has hitherto been found. In one

of the "Challenger" dredgings the species is by no means uncommon, but owing to the loose crumbling character of the test, nearly every specimen is more or less broken and much in the condition of that represented in fig. 19 of the same plate. A number of individuals, apparently belonging to the same species, have been met with, bearing only three or four segments. These are generally of smaller size, and are composed of finer sand-grains; the segments have the normal globular shape, but they are more symmetrically arranged.

The distribution of *Sorosphæra confusa* appears to be somewhat local, but in areas wide apart. It occurs amongst the "Challenger" gatherings at one station in the North Atlantic (off the Azores, 900 fathoms), at one in the South Atlantic (off Buenos Ayres, 1900 fathoms), and at two points near together in the North Pacific (2050 and 2900 fathoms respectively), and I have also met with it in one of the "Porcupine" soundings in the North Atlantic.

Genus—PELOSINA, *nov.*

(πηλός, mud.)

General Characters.—Test free, one- or many-chambered, with walls composed of a thick layer of mud, terminating in an elongate chitinous neck.

PELOSINA VARIABILIS, *n. sp.* Pl. III, figs. 1, 2, 3.

Characters.—Test consisting of a single chamber, or of several independent (?) chambers irregularly associated. Segments unsymmetrical, variable in shape, generally rounded, elongate and tapering. Walls thick, composed of fine mud deposited on a chitinous (?) basis, which is usually extended beyond the body of the test as a sort of neck. Aperture terminal. Size of the individual segments variable, sometimes $\frac{1}{3}$ inch (8 millim.) or more in length.

It is not easy to determine with any certainty the affinities of the shapeless or irregularly shaped muddy organisms which have been placed together under the generic name *Pelosina*. That they are inhabited by sarcode animals is known, but what common characters they may have, sufficiently permanent and distinctive to serve as the basis of a zoological group—generic or even specific—is not so manifest. Of the larger Rhizopoda, perhaps *Astrorhiza limicola* presents the nearest parallel in the employment of indiscriminate mud as the material for the construction of its investment, and the same species presents an example of the com-

parative absence of any kind of cement or other incorporating medium for the extraneous matters which are used in forming its walls. Hence the test is soft and crumbling and the requisite strength is obtained by increased thickness, and it is never compact enough in texture to be spoken of as a "shell."

What the precise nature of the membranous tubular prolongations of the test may be, whether they are part of a definite chitinous envelope or merely the superficial portion of the sarcode in a somewhat altered condition, has not been satisfactorily determined. The genus *Astrorhiza* again furnishes us with the nearest parallel. The specimen of *A. cornuta* (Pl. IV, fig. 15) has tubular membranous extensions from the ends of the branches, not always simple, as in *Pelosina*, but usually bifurcating; and in a large undescribed species of the former genus of which I have a specimen, dredged by Mr. F. M. Balfour in the North Sea, a considerable portion of the body of the animal has a membranous investment, only slightly sprinkled with sand-grains or mud. These facts tend to indicate that *Pelosina* should have a place very near to *Astrorhiza* in the zoological series.

The best specimens of *Pelosina variabilis* amongst the "Challenger" deep-sea spoils are from a sounding on the east side of New Zealand, in 1100 fathoms, but single specimens have been met with in several other localities.

PELOSINA ROTUNDATA, *n. sp.* Pl. III, figs. 4, 5.

Characters.—Test consisting of a single flask-shaped or pyriform chamber, with produced membranous neck. Walls thick composed of muddy *Globigerina*-ooze. Diameter, $\frac{1}{15}$th inch, (2 millim.).

This species differs from *P. variabilis*, in that it consists uniformly of a single subglobular or pyriform chamber, and that it is usually of smaller dimensions. The walls are relatively very thick, and are composed of soft, greyish-white, muddy material, with scarcely any incorporating cement. It naturally follows that the central cavity occupies but a very small proportion of the entire bulk of the test.

Pelosina rotundata appears to be essentially a North Atlantic species. Amongst the "Challenger" dredgings I have only found it from one station, namely, off the Azores, in 1675 fathoms, but it occurs in one of the "Porcupine" soundings in much shallower water, 109 fathoms.

Genus—HYPERAMMINA, *Brady*.

General characters.—Test free or adherent, elongate, tubular; primordial end closed and rounded; opposite extremity open and unconstricted, forming the general aperture. Texture arenaceous, interior smooth.

HYPERAMMINA ELONGATA, *Brady*.

Hyperammina elongata, 1878. 'Annals and Mag. Nat. Hist.,' Ser. 5, vol. i, p. 433, pl. 20, fig. 2 *a*, *b*.

Characters.—Test free, in the form of a straight, or nearly straight, unbranched, tapering tube; the wide end closed and rounded, the narrow end constituting the general aperture. Exterior either loosely sandy or compact and smooth, rarely polished. Length up to ½ an inch or more (15 or 16 millim.).

Amongst the dredged sands brought home by Capt. Feilden from the recent North Polar Expedition were one or two specimens of this somewhat striking type. Compared with examples from less boreal latitudes they are very small and not such as can be regarded as average representatives of the species, and for this reason the drawings which accompany the description of them, though quite accurate, must be accepted with some allowance until a series of more characteristic figures can be furnished. The type was by no means unknown previously, inasmuch as fine specimens had been found in dredgings made by the staff of the "Porcupine" in the North Atlantic, and in material obtained by the "Challenger" at various stations both in the North and South Atlantic and in the North and South Pacific.

The texture of the test in *Hyperammina elongata* is somewhat variable. In large specimens it is usually loose and sandy, but the sand-grains being fine and of nearly even size, the exterior is, notwithstanding, tolerably smooth. Small individuals are generally much longer in proportion to their diameter than the larger ones; they are often darker coloured, and their exterior is usually quite smooth or even polished. The interior in all cases is smooth and often stained brown, either by animal secretion or by the adherent remains of dark coloured sarcode. This colouration is quite distinct from the general yellowish hue of the test, which is determined by the presence of small quantities of peroxide of iron. As has been before stated, the geographical distribution of *Hyperammina elongata* is very wide, and this is equally true of its bathymetrical range, but though the species has been met with at depths up to 2600 fathoms, the

largest specimens have been found in dredgings from 300 to 500 fathoms.

HYPERAMMINA RAMOSA, *n. sp.* Pl. III, figs. 14, 15.

Characters.—Test free; consisting of a subglobular primordial chamber with a tubular extension. Tubular portion branched; relatively wide at its commencement, but narrowing as it becomes divided. Texture usually loosely arenaceous; exterior rough, often beset with sponge-spicules. Length indefinite.

This organism, though manifestly allied to the typical form last described, differs from it in several important particulars. The test never attains the same dimensions as the larger examples of *Hyperammina elongata*. The texture is generally coarse, and the surface is commonly rough, or even hispid, with the sand-grains and partially incorporated sponge-spicules used as building material. Instead of tapering uniformly from the rounded end, the test is constricted near its commencement, so as to form a more or less bulbous primordial chamber. The tubular limb issuing from this is branched instead of simple, wide at first, but narrowing as it becomes more and more divided. The finer ramifications are exceedingly thin and fragile, and it is impossible to say what length they may attain.

The distribution, both geographical and bathymetrical, of *Hyperammina ramosa* is very similar to that of *H. elongata* already described. The two species are very often, though by no means invariably, found in the same batches of dredged material. Fragments of delicate branching arenaceous tubes belonging to this or some analogous form are exceedingly common in deep-sea material, though they often cannot be identified with certainty.

HYPERAMMINA VAGANS, *n. sp.* Pl. V, fig. 3.

Characters.—Test more or less adherent; consisting of a spherical primordial chamber opening into a long, usually unbranched tube, of nearly even diameter, sometimes partially free, but commonly spreading in irregular tortuous lines over the surface of shells, stones, or other foreign bodies, the open unconstricted end of the tube serving as the general aperture. Walls thin; texture finely arenaceous; surface smooth but not polished. Colour brown, the primordial chamber usually of darker hue than the tube. Length indefinite.

In some areas the fine arenaceous tubes of this or other similar Rhizopod are found to a greater or less extent on

almost every fragment of shell or stone presenting a surface favorable to their growth. It is rarely, however, that the tests are even approximately complete or perfect, and the primordial chamber being generally the missing portion they have hitherto been passed over, under the supposition that they were the tubes of adherent annelids. This imperfection arises from the fact that the primordial chamber is seldom completely attached to the body on which the remainder of the test is adherent. The tubular portion of the test is of indefinite length and always seeks some solid basis to spread itself upon, in the absence of which it is occasionally found in little masses formed of irregular coils adherent to each other. The bulbous end is often quite free, projecting above the remainder of the test, from which it does not otherwise differ in external characters, except that it is of a darker reddish-brown colour.

Hyperammina vagans differs from both *H. elongata* and *H. ramosa* in its parasitic habit; from the former also in the great length and tortuous course of the tubular portion, and from the latter in the simple unbranched contour of its extensions. There is only one Foraminifer, so far as I know, with which it is at all likely to be confounded, namely, *Webbina cirrata*, P. and J., but the primordial chamber in that species is a simple, adherent, tent-like, shelly dome, and the tube a semi-cylindrical covering, neither of which has any floor proper to itself.

There is a fossil organism, occasionally met with in palæozoic limestones of considerable interest in connection with this species. It consists of rounded masses of finely arenaceous tubes folded irregularly backwards and forwards, or otherwise coiled, so as to form little bundles. My friends, Prof. H. A. Nicholson, and Mr. R. Etheridge, jun., have recently called my attention to some of these, which exist in large numbers in the Silurian rocks of Girvan in Ayrshire, and they will, I believe, be described in their forthcoming 'Monograph of Girvan Fossils,' under the provisional generic term *Girvanella*. When the time comes for treating the "Challenger" Rhizopoda in detail, I shall be able to give drawings of specimens of *Hyperammina vagans*, which scarcely differ from the palæozoic fossil except in their somewhat larger size.

For the most part *H. vagans* is a deep-sea species, the finest specimens being from two dredgings in about 2000 fathoms, one in the North Pacific, the other in the South Atlantic, but it occurs also at smaller depths, especially in the North Atlantic.

Genus—JACULELLA, *nov.*

JACULELLA ACUTA, *n. sp.* Pl. III, figs. 12, 13.

Characters.—Test elongate, straight or nearly so, closed and pointed at one extremity, gradually increasing in width towards the other, which, slightly constricted and rounded, but otherwise open, forms the general aperture. Texture arenaceous, very compact, and hard; exterior surface rough, interior also rough, but in a less degree. Colour rich brown in the earlier portion of the test, becoming gradually lighter towards the wide end. Length $\frac{1}{3}$ inch (8·5 millim.).

It is often an exceedingly difficult matter to determine whether the tubular, non-septate, arenaceous tests, so frequently met with in certain localities and in such diverse forms, have belonged to sarcode animals or to annelids, and there is unfortunately no character short of those pertaining to the live inhabitant that can be regarded as certain evidence. Annelid tubes of the commoner species are easily recognised, and so also are the cylindrical tests of Rhizopoda when they are either septate or labyrinthic, or show a distinct primordial chamber; but many of the specimens alluded to, both arenaceous and porcellanous, present none of these features, and the decision rests on probabilities rather than positive indications.

These remarks apply with some force to the species now under consideration. The specimens were selected from a number of doubtful organisms, as probably of Rhizopod origin, on the strength of two or three characters which, taken together, were thought to have considerable weight. The first of these was the firmly arenaceous texture of the test, then the distribution of colouring matter which, as in *Hyperammina vagans* and several other species, is of deep brown red in the early portions and gradually becomes lighter, and, lastly, a fact of negative value, namely, that the rough interior appeared ill-adapted for the organisation and life conditions of an annelid. Not trusting my own opinion on the matter, I submitted some of the tests to Dr. McIntosh, the recognised British authority on the *Annelida*, who after examining them, expressed a very decided belief that they did not belong to animals of that group. On the other hand, there is no other non-septate type of Rhizopoda with a test increasing so rapidly in diameter, and with an aperture relatively so large; and, again, almost every specimen, if not every one, has a minute orifice at the narrow end. The

first of these objections is of little real weight, and the second may depend on accidental breakage, a not improbable occurrence under the circumstances. Whilst still hesitating about my specimens the Rev. A. M. Norman had obtained the same species in his dredgings from the coast of Norway,[1] and, without knowing that I had been working upon it, had assigned it in his own mind to the Foraminifera. He suggested the name *Jaculella* as applicable to the genus, and I am very glad to adopt it.

The form and general appearance of *Jaculella acuta* is shown in Pl. III, fig. 12; and fig. 13 represents a specimen ground down to show the interior. As has been said, it is exceedingly rare to find a large individual with the thinner extremity perfect, and the test is so hard and brittle that it breaks away still more in process of grinding.

The largest specimens of this species which have been met with in the "Challenger" material are from Station 122 (off the coast of Brazil, 350 fathoms), and some of these are a third of an inch or more in length. Its range of distribution can hardly at present be satisfactorily laid down.

Genus.—MARSIPELLA, *Norman*.

MARSIPELLA GRANULOSA, *n. sp.* Pl. III, figs. 8, 9.

Charàcters.—Test free, fusiform, tapering nearly equally towards both ends; composed of fine grey sand, with very little calcareous cement. Cavity nearly uniform in diameter; walls thickest in the middle of the test. Exterior granular, interior nearly smooth. Apertures simple, one at each end of the test often tinged brown. Length $\frac{1}{5}$ inch or more (5 or 6 millim.).

Amongst the Rhizopoda of the "Porcupine" Expedition is a very striking species, common in certain areas, having an elongate, fusiform test, often curved and twisted, especially near the extremities, and usually tapering more rapidly at one end than at the other. The test is formed of sand-grains neatly fitted together, or, especially near the ends, of acicular sponge-spicules, laid side by side and united by just sufficient calcareous cement to produce a firm investment. The extremities are both open, and serve as pseudopodial apertures. Dr. Carpenter assigns this form to Williamson's

[1] Mr. Norman also tells me that he dredged *Jaculella* in St. Magnus' Bay, Shetland, in about 60 fathoms, in 1867, and it thus becomes an addition to the British Fauna.

genus *Proteonina*.[1] The Rev. A. M. Norman, in his interesting paper on *Haliphysema* and forms apparently allied to it[2] has thrown much light on the group to which the "Porcupine" species probably belongs, and discarding the supposed affinity to the so-called *Proteonina*, which is a feeble Lituoline form of the *Haplophragmium* series, has given it the new generic name, *Marsipella*. In this course I entirely concur.

As the occurrence of *Marsipella elongata*, Norman, is pretty much confined to areas in the Atlantic, further north than any point in the line of the "Challenger" cruise, its history need not be dwelt upon here, but a form which appears more nearly allied to it than to any other described type is occasionally met with in southern latitudes. This I propose to call *Marsipella granulosa*. It agrees with *M. elongata* in its fusiform contour, and in having an aperture at each extremity of the test, and these perhaps may be regarded as the essential characters of the genus. On the other hand, the test is composed entirely of fine sand, and it is much less compactly built than that of *M. elongata*, the walls being thick in the middle and thinning away towards the ends. A specimen, laid open, is shown in Pl. III, fig. 9, but portions of the slender extremities have crumbled away in the process of grinding. Figure 8, of the same plate, represents a nearly perfect individual. The material selected for the construction of the test, in the absence of sponge spicules, is an even-grained, light-coloured, very fine sand, and as the amount of cement (whatever it may be) secreted by the animal is very small, the requisite solidity appears to be attained by the thickening of the walls, and this takes place to such an extent that the central cavity is little more than a tube of nearly even diameter. The interior is smooth and stained reddish brown to a greater or less degree, and the same colouration is also apparent externally at the extremities of the test around the orifices.

The best specimens of *Marsipella granulosa* have been found in a dredging off the Azores, at a depth of 1000 fathoms.

Genus—RHABDAMMINA, *M. Sars.*

RHABDAMMINA LINEARIS, *n. sp.* Pl. III, figs. 10, 11.

Characters.—Test free, linear; straight or curved; con-

[1] Carpenter, 'The Microscope,' fifth ed., 1875, p. 533, fig. 273, *d. e. f.*;—Williamson, 'Rec. For. Gt. Br.,' p. 1, pl. 1, figs. 1—3.
[2] 'Annals and Mag. Nat. Hist.,' ser. 5, vol. i, p. 281, pl. 16, fig. 7.

sisting of a cylindrical arenaceous tube, with swollen centra chamber. Tubular portion often irregular in outline, tapering towards the ends; shell-wall of the central chamber thinner than that of the two arms. Length $\frac{1}{4}$ inch (4·5 millim.).

Amongst the types of arenaceous Rhizopoda enumerated by the lamented Scandinavian naturalist, Michael Sars, in the short paper summarising the results of his deep-sea researches,[1] is a fine large species, which he names *Rhabdammina abyssorum*. In the absence of any description from the pen of the discoverer it may be characterised as having a radiate test, consisting of three to five long arenaceous tubes, diverging from the central point like the spokes of a wheel. In specimens from some localities there is a small central chamber, and in these cases the arms are broad at the point of insertion and somewhat tapering, but more frequently the arms are of nearly even diameter, and there is little or no swelling at the point of union. Generally speaking, the tubular portions radiate on one plane and the test is complanate, but sometimes this order is not observed, and they diverge irregularly. Specimens of *Rhabdammina abyssorum* from the southern hemisphere do not differ in any important particular from those obtained by Sars from a depth of 450 fathoms off the Norwegian coast. Under favorable conditions the species attains a considerable size, but owing to the tenuity and brittleness of the rays it is seldom, probably, that specimens are quite perfect; examples, however, are not uncommon that must, when complete, have measured an inch from point to point.

In three or four of the "Challenger" dredgings there is found a much smaller form referable to the same genus, but with sufficiently distinctive characters of its own, and this I propose to name *Rhabdammina linearis*. It may be regarded as a two-rayed modification of the type, with a central inflated cavity. The two arms are seldom of the same diameter, nor are they usually set on so as to form a right line. In texture the test is more loosely built, and the sand-grains less completely incorporated, than in the typical species. In light-coloured specimens the extremities are sometimes stained reddish brown.

The mere fact of possessing but two arms instead of three, four, or five, would not by itself constitute a valid reason for distinguishing a variety by name, especially if it were found in company with the radiate form; but, taken in conjunction

[1] 'Vidensk.-Selsk. Forhandinger' for 1868.

with its much smaller size—often not $\frac{1}{10}$ in. in entire length—and its occurrence in localities in which the other is not found at all, there can be little doubt of its title to a distinctive appellation.

The best "Challenger" specimens of *Rhabdammina linearis* have been obtained from dredgings off Sombrero Island and off Culebra Island (West Indies) in 450 fathoms and 390 fathoms respectively, and from a deeper sounding (1900 fathoms) off the coast of South America, in latitude 35° 59′ S.

Genus—RHIZAMMINA, *nov.*

(ῥίζα, a root; ἄμμος, sand).

RHIZAMMINA ALGÆFORMIS, *n. sp.* Pl. IV, figs. 16, 17.

Characters.—Test free, tubular, branching, flexible; forming tangled weed-like tufts of indefinite size. Texture chitino-arenaceous, slightly rough externally; colour brown.

Amongst the doubtful organisms which have from time to time been dredged in deep-water in various parts of the world, minute, branching, flexible tubes, with rough exterior from embedded sand-grains, have not been the least frequent. These have hitherto occurred in comparatively small numbers, and though they have been supposed to belong to the Rhizopoda, their precise nature has not, as far as I am aware, been investigated. At one of the "Challenger" stations off the western coast of South America, in about the latitude of Valparaiso, the principal part of the contents of the dredge consisted of a weed-like organism of this sort.

At first sight its tangled threads bear considerable resemblance to masses of some Melanospermous Alga, such as *Stilophora rhizodes*, but quite apart from the fact that the sarcode animal was observed whilst still in fresh condition, the structure of the investment of the preserved specimens is sufficient to determine its Rhizopod affinities. My friend Mr. Hollick has not been quite so successful as is his wont, in the figure representing a bit of the organism of the natural size (Pl. IV, fig. 16), but the enlarged drawing (fig. 17) gives very accurately the appearance of a portion of one of the younger and more transparent branches mounted in Canada balsam.

When spread out on a white surface the mass is seen to be composed of branching tubes, varying in diameter from $\frac{1}{\cdot 1 7 7}$ to $\frac{1}{\cdot 7 8}$ of an inch (0·53 to 0·32 millim.). What their

original length may have been it is impossible to say, but it is seldom that pieces can be separated of more than an inch or an inch and a half long. There is no evidence that it has grown attached to any foreign body, though it is quite possible that it may have done so. The branching does not take place on any definite plan. Entangled amongst the branches are often fragments of Polyzoa and other similar organisms.

Notwithstanding the flexibility and apparent softness of the tubes, the proportion of organic matter they contain is relatively very small. A mass of the "weed," thoroughly washed to free it from soluble saline matter, and dried at 100° centigrade, left 87·6 per cent. of ash after ignition, and this was almost entirely composed of silica. When living, or in the fresh condition, the proportion of inorganic constituents would necessarily be a good deal smaller, but the amount of moisture normally present in the test could not be estimated from specimens which had been preserved for a long period in alcohol. Under the microscope the appearance of the tubes would give the idea that the chitinous or organic basis formed a much larger proportion of the entire weight. The arenaceous constituents are partly in the form of minute angular sand-grains embedded in the chitinous envelope but sufficiently exposed to give the surface a distinctly rough appearance, and partly of the empty siliceous tests of Radiolaria, which abound in the mud of the sea-bottom in this particular locality.

Boiling in water has no appreciable effect on the organism in the condition in which it has come into my hands, that is, after long maceration in alcohol; and moderately strong acetic acid produces no perceptible change in it, even on the application of heat. Heated in dilute hydrochloric acid (1—4) there is at first a slight effervescence, carbonic acid being evolved from a few minute Foraminifera built into the test rather than from any calcareous cement, of which there appears to be little or none. Under the influence of hydrochloric acid most of the tubes break up, and eventually become entirely disintegrated, owing apparently to the solution of the organic matter. In those which remain the test appears as a colourless sandy envelope, and the sarcode, which has swollen to its original size, as a granular, transparent brown mass, filling the cavity of the tube. With nitric acid (1—4) the disintegration is much more rapid, and after a time there is but little residue beyond the siliceous constituents.

Treated with caustic potash and heated, the tubes are considerably disintegrated, but in a different way. Those that

retain their form are split and empty, as though the contents had swollen to bursting before being dissolved out. Digestion in these cases was not carried far enough to dissolve much of the siliceous matter, and the split tubes therefore represented the inorganic portion of the investment.

There is no other Rhizopod to which *Rhizammina* can be very accurately compared, but it has perhaps most in common with the branching tubes of *Hyperammina vagans:* in point of fact, it represents a very distinct type of organisation.

The locality alluded to, in which it is so abundant, is the "Challenger" Station, No. 299, lat. 33° 31′ S.; long. 74° 43′ W.; that is, between the Island of Juan Fernandez and the western coast of South America; depth 2160 fathoms.

Genus—SAGENELLA, *nov.*

(σᾰγήνη, a drag-net).

SAGENELLA FRONDESCENS, *n. sp.* Pl. V, fig. 1.)

Characters.—Test adherent; consisting of long, finely arenaceous covered passages, ramifying or forming a network over the surface of shells or other bodies. Branches bifurcating, each limb terminating in a neatly rounded aperture. Colour white to very light brown. Length indefinite; diameter of the larger passages $\frac{1}{60}$ inch (0·4 millim.) of the smaller branches $\frac{1}{200}$ inch (0·12 millim.).

This singular little organism occurs amongst the Nullipore *débris* of shallow water in the South Pacific, in company with other parasitic Rhizopoda, such as *Placopsilina*, *Planorbulina*, and *Truncatulina*. There is possibly no other known instance of a Foraminifer with a distinctly reticulating test, either free or adherent, but it is not difficult to understand how the inosculation of the passages takes place. The branches commonly bifurcate at their extremities, and each fresh branchlet, after growing about a thirtieth of an inch, more or less, divides again in the same way; thus, however irregular the growth, the sarcode projecting from the different apertures must continually meet, and the ends naturally coalesce; the investment being formed as growth proceeds, an irregular shelly network of necessity results. The test is very finely arenaceous, and it appears to be really tubular, that is to say, it is not a mere tent-like covering without a floor proper to itself, like that of *Webbina*. It occurs in little patches a quarter of an inch or more in diameter, of white or light yellowish-brown colour. The ends of the

branches are seldom perfect, owing to their delicate nature, but when they have been accidentally protected and remain complete, they show smooth, rounded apertures formed of clear shell-substance.

The best specimens of *Sagenella frondescens* have been found in Nullipore dredged off the Admiralty Islands, at a depth of from 16 to 35 fathoms.

Genus.—ASTRORHIZA, *Sandahl.*

Astrorhiza, Sandahl, M. Sars, Carpenter, Norman.
Haeckelina, Bessels.
Astrodiscus, F. E. Schulze.

ASTRORHIZA CATENATA, *Norman.* Pl. IV, figs. 12, 13.

Astrorhiza catenata, Norman, 1876. 'Proc. Roy. Soc.,' vol. xxv, p. 213.

The Rev. A. M. Norman (loc. cit.) describes this species in the following words:—"The chambers are more or less ovoid, not flattened, as in the previously known forms, but equally rounded on the sides and above and below; the spoke-like pseudopodian processes, instead of being all on one plane, as in *A. limicola*, radiate in all directions. Several specimens occurred in which two chambers were united together, a fresh chamber being developed at the end of one of the radiating processes; and it is probable that, in its most perfect state, the animal would consist not only of a series of chambers extending on all sides, as in *A. limicola*, but of other chambers superimposed on these, so that the whole animal would be of most complex type. The arenaceous investiture consists of fine sand-grains and sponge-spicules firmly (not loosely, as in *A. arenaria*) cemented together, and is of a ruddy hue, but not ferruginous, *Astrorhiza catenata*, *n. sp.*, may be the name to distinguish this animal."

My friend Mr. Norman has recognised the two figures (Pl. IV, figs. 12, 13) as pertaining to his species, a fact which had not suggested itself to me, so little impression does verbal description, unaccompanied by drawings, make upon the mind in such cases. I should have had much hesitation in placing my own specimens in the same genus with either the muddy, discoidal, radiate *Astrorhiza limicola*, or with an organism having the thick, soft, sandy walls and flat branching contour of Dr. Carpenter's species; but their number is small, and they scarcely afford a means of forming a confident opinion; at any rate I am not prepared to debate the point in opposition to the views of so experienced a zoologist. The largest example in my collection is less than

$\frac{1}{10}$ inch (2·5 millim.) in entire length; it has two segments, and appears to have had a third. Either of the other species attains many times this size. The walls are thin, compact, and brittle, and, as stated in the description, are largely made up of sponge spicules.

The "Challenger" dredgings have yielded specimens from the South Pacific (2760 fathoms) and from the North Atlantic (West Indies, 290 fathoms); Mr. Norman's were from the material obtained on the cruise of the "Valorous" (off Greenland, 1350 fathoms); and others have been found at one at least of the "Porcupine" stations in the North Atlantic (1215 fathoms).

ASTRORIZA CORNUTA, *n. sp.* Pl. IV, figs. 14, 15.

Characters.—Test free, irregular; outspread or rounded, with branching or tapering radiating processes; interior following the same general form as the test; non-septate. Branches either terminating in simple apertures, or furnished with simple or bifurcating, open, chitinous tubes, which serve the same end. Exterior very rough, composed of coarse sand-grains firmly cemented together. Size, ranging from $\frac{1}{20}$ inch (1·25 millim.) in the rounded forms, to $\frac{1}{5}$ inch (5 millim.) in the outspread varieties.

Accepting the view that the organism last described really belongs to the genus *Astrorhiza*, there can be little doubt that the specimens represented in Pl. IV, figs. 14, 15, also pertain to the same group; indeed, they exhibit something like the mean of the characters of *A. arenaria* and *A. catenata*. Many of the specimens have very much the contour of the former species, and differ from it principally in shell texture, whilst some of the rounded forms are chiefly distinguishable from *A. catenata* by possessing only a single chamber when fully grown. As may be inferred from what has been already said, the thick, loosely-aggregated test appears to me to furnish the most significant character of *Astrorhiza limicola* and *A. arenaria*, and therefore the affinity of the species now described is with *A. catenata* rather than with these.

Specimens of *Astrorhiza cornuta* have been found at two of the "Challenger" stations, namely, in the South Atlantic, off Pernambuco, 350 fathoms, and in the South Pacific, off New Zealand, 1100 fathoms; examples also occur at one of the "Porcupine" stations in the North Atlantic, in 816 fathoms.

Genus—ASCHEMONELLA, *nov.*

(ἀσχήμων, of ugly shape).

ASCHEMONELLA SCABRA, *n. sp.* Pl. III, figs. 6, 7.

Characters.—Test free, consisting of one or more chambers of irregular size and shape. Chambers inflated, often with more than two tubulated apertures, any of which may produce a fresh segment. Walls thin, compactly built; exterior slightly rough, sometimes acerose with partially embedded sponge-spicules. Segments variable in size; length $\frac{1}{8}$ inch (3 millim.), more or less.

This is a type the nature and affinity of which it is very difficult to comprehend. The form and size of the segments might almost seem to be a matter of accident, and yet when a number are seen together they bear a quite unmistakable general resemblance to each other, not only in shell-texture and substance, but in their habit of growth. It is impossible to describe the multiplicity of forms the chambers assume. Sometimes they are elongate, straight or curved tubes, with rounded or tapering ends, either unconstricted or constricted at intervals, as though tied up crookedly. More commonly, instead of the two terminal apertures, that the chambers of polythalamous Foraminifera usually present, the lobes have three or four, or even five, tubulations, any one of which may give rise to a new segment, for which it forms the stoloniferous passage. Very often the segments are forked, and each branch terminates in an aperture. A large proportion of the specimens have only one chamber, but probably this is in part due to fracture, the connecting tubes being narrow and slender in proportion to the weight of the lobes, but many have two, and occasional examples have been found with three, segments. In point of size the variation is equally marked; the individual segments vary from very small dimensions up to one fifth of an inch or even more in length.

Aschemonella scabra is by no means a common species, though it occurs sparingly at several of the "Challenger" stations. It appears to affect deep water, for of the six localities in which it has been found all have recorded depths of 1000 fathoms or more, and half of them of over 2000 fathoms. Two of these stations are in the North Atlantic (off the Azores and south-west of the Canaries), one in the South Atlantic (east of Buenos Ayres), and three in the North Pacific.

Genus—THURAMMINA, *nov.*

(θυρίς, a cell; ἄμμος, sand).

General characters.—Test free or adherent; either consisting of a single rounded chamber, sometimes enveloping a similar one of smaller size, or of two or more (apparently) independent chambers adhering to each other. Texture thin; arenaceous or chitino-arenaceous. Surface beset with numerous, perforate, nipple-shaped protuberances.

THURAMMINA PAPILLATA, *n. sp.* Pl. V, figs. 4—8).

Orbuline *Lituola*, Carpenter, 1875, 'The Microscope and its Revelations,' Fifth Ed., p. 533, fig. 273, *g. h.*

Characters.—Test free or adherent; usually consisting of a single spheroidal chamber, with or without an elongated neck; occasionally of two or more of such chambers mutually adherent. Surface studded with irregularly disposed perforate papillæ. Colour brown; shell-wall, very thin, composed of light-coloured sand-grains fitted together accurately with reddish-brown cement. Diameter of the chambers $\frac{1}{50}$ inch (0·5 millim.), more or less.

Dr. Carpenter (loc. cit.) gives a partial description of this type, founded apparently on an insufficient number and variety of specimens, to yield a clear sense of its morphological range. The shell represented by fig. 4 (Pl. V) gives a fair idea of its usual contour and condition, but it frequently happens that the neck is wanting, and in such cases there is no general pseudopodial aperture distinct from the orifices of the papillæ. Occasionally the test is adherent either to a piece of shell, as in fig. 5, or to some other foreign body, and then the shape is altered to meet its changed relations. Sometimes two or three chambers are found adherent to each other, as in fig. 8, but in such cases the individual segments appear to retain their independence, and not to assume with each other a corporate existence as a single polythalamous organism. That is to say, the polythalamous condition depends on the adhesion of spheres by their contiguous surfaces rather than on the segmentation of sarcode and the formation of connecting stolons with corresponding shelly investment. Occasionally, though rarely, on breaking the test a second smaller chamber with papillate projections is found in the interior; such an example is seen in fig. 6, and a primordial chamber of this sort from another shell is shown in fig. 7.

The minute structure of the shell-wall is very beautiful.

It is formed of angular sand-grains accurately fitted to each other and held together with a dark reddish-brown cement.

The number and degree of prominence of the nipple-like projections vary very much. In some specimens they are very numerous and striking, and they are often arranged in a sort of linear order; in others they are much less conspicuous, and are irregularly distributed. They are probably all perforated, but the apertures are often very obscure.

The distribution of *Thurammina papillata* is world-wide. The "Challenger" collections furnish specimens from both the North and South Atlantic and the North and South Pacific. Of ten localities in which I have record of its occurrence, five are from depths of more than 2000 fathoms, and only three of them less than 1000, the shallowest of all being 350 fathoms, so that it may be regarded as an essentially deep-water type.

THURAMMINA ALBICANS, *n. sp.*

Characters.—Test free, monothalamous, nearly spherical, with few (4 or 6) mammillate orifices, equidistant and regularly disposed. Texture very finely arenaceous, colour white. Diameter $\frac{1}{100}$ inch (0·25 millim.).

A few specimens of a very minute organism, apparently allied to the foregoing species, have been found in several of the "Challenger" dredgings. The test is much smaller than that of *Thurammina papillata*, the shell-wall relatively thicker and composed of finer materials, and the little mammillate protuberances, instead of being numerous and distributed irregularly over the surface, are few in number and placed symmetrically. The figures of this form have unfortunately had to be omitted for want of space.

Single specimens have been met with in many samples of deep-sea material. Perhaps the best series is from 1900 fathoms, off the coast of South America, in about the latitude of Buenos Ayres.

THURAMMINA COMPRESSA, *n.sp.* Pl. V, fig. 9.

Characters.—Test free, monothalamous, compressed; with numerous perforate, mammillate protuberances arranged irregularly on the periphery. Walls thin, chitino-arenaceous; colour dark-brown. Diameter, $\frac{1}{50}$ inch (0·5 millim.).

This is another form, rarely met with, apparently nearly related to *Thurammina papillata*. Its chief distinction rests on its membranous, only slightly arenaceous, shell-texture, and its compressed lenticular contour. It is just possible that the latter character may be in a measure accidental, and be

due to the partial collapse of the investment, as not unfrequently occurs in certain other chitino-arenaceous forms, *Trochammina macrescens*, for example. The mammillate orifices do not appear on the upper and lower surfaces, but only on the peripheral portions of the test.

The figured specimen is from the North Atlantic ("Porcupine"), 109 fathoms.

Genus—LITUOLA, *Lamarck*.

In the 'Introduction to the Study of the Foraminifera,' published in 1862, all the then-known Foraminifera having sandy or composite tests are referred to three genera—*Lituola*, *Trochammina*, and *Valvulina*, the last named being regarded as an intermediate rather than as a strictly arenaceous type. To *Lituola* are assigned all the *rough* arenaceous forms, whatever their external contour or the condition of the interior of their chambers; and to *Trochammina* those in which the constituent sand-grains are small and incorporated by a large excess of calcareous or ferruginous cement, a thin, *smooth*, non-labyrinthic shell being the result. This simple classification answered every end so long as the number of forms to be accommodated and their known range of variation were comparatively limited, and there can be no doubt that it touched the essential distinction between two of the principal groups of this section of the Rhizopoda. But in the present state of our knowledge it scarcely meets the requirements of the case. Not only have a large number of arenaceous species been found with generic characters very different from those of either of the types thus defined, but the number of new forms and varieties, possessing the same peculiarities of shell-structure as *Lituola* and *Trochammina* respectively, has been so multiplied that the subdivision of both groups has become desirable, if not necessary. The arrangement of the *Trochamminæ* is considered on a subsequent page, and although I have but little that is new to bring forward relating to *Litulola* (proper), it is quite within the plan of the present paper to state briefly the results which have been arrived at from the study of the very large series of forms furnished by the "Challenger" dredgings.

Practically the genus *Lituola*, as understood in this country, has been coextensive or thereabouts with Professor von Reuss's family *Lituolidea*, which is made to include four genera, characterised as follows:

1. *Polyphragma*,[1] Reuss.—Test adherent.

[1] *Polyphragma cribrosum*, Reuss, as figured in 'Das Elbthalgebirge in Sachsen,' 1ter Th., 1872, p. 139, pl. 33, figs. 8—10, has an irregular,

2. *Haplophragmium*, Reuss.—Test free, chamber-cavities simple, not subdivided.
3. *Lituola*, Lamarck.—Test free, chamber-cavities subdivided by irregular ramifying septa; spiral or crozier-shaped; aperture dendritic, labyrinthic or compound.
4. *Haplostiche*, Reuss.—Test free, uniserial, straight or arcuate (like *Nodosaria*, or *Dentalina*); aperture terminal, simple. Chamber-cavities subdivided by irregular ramifying septa.

The term *Lituola* was originally used by Lamarck[1] for the well-known subnautiloid and crozier-shaped, white, arenaceous Foraminifera of the Chalk; and as d'Orbigny adopts Lamarck's name,[2] making the labyrinthic chambers and multiple aperture the primary characters of the genus, there can be no doubt as to its proper application.

In the difficulty that there is of finding characters available for the classification of a series of forms so closely connected as those under consideration, the structure of the shelly skeleton must serve as far as it goes, as a basis of subdivision. It is, however, to the interior of the test that we shall have to look for its most characteristic development. In some of the Lituoline forms the chambers are simple rounded cavities, and the sand-grains of which the test is built are often so neatly joined that no angular points project into the interior. Such specimens have generally a simple aperture. In others the interior of the segments is "labyrinthic," that is to say, subdivided by irregular partial septa, composed of rough sand grains cemented together, and such as these commonly have an irregular or compound aperture. There is another variety of labyrinthic structure, that may for distinction be called "cancellated," which is composed of masses of very finely arenaceous tubular growths from the inner surface of the shell-wall, sometimes developed to such an extent that they almost fill the cavities of the chambers. But as specimens with this peculiarity have at the same time a smooth or even polished exterior and very definite and well-formed septa, it is manifestly better to keep them distinct

elongated, straight or curved, subcylindrical test, adherent by its expanded lower extremity, composed of a single series of thin chambers superimposed, and having a terminal aperture consisting of numerous large perforations. It is an Upper Cretaceous fossil from the "Unter Pläner" of Bohemia, Saxony, and elsewhere.

[1] 'Annales du Muséum,' 1804, vol. v, p. 242; figured in 1816 in vol. viii, pl. 62, fig. 12, and elsewhere.

[2] 'For. Foss. Vienne,' p. 138, pl. 21, figs. 20 and 21.

from the *Lituolæ*, and a separate genus has been constituted for them.[1]

The generic term *Reophax* was employed by De Montfort, in 1808,[2] for an irregular scorpioid, moniliform *Lituola*, with rough exterior and simple undivided chambers. His figure is copied from one of Soldani's,[3] and as it represents a good typical example, there seems no reason why the name should not be retained for the non-labyrinthic uniserial group.

For the parasitic or adherent modifications, d'Orbigny's generic appellation, *Placopsilina*,[4] is already to some extent employed todesignate the common non-labyrinthic forms, and Mr. Carter has described under the name *Bdelloidina*[5] an adherent arenaceous organism apparently of more complex type, which occupies a similar position in the labyrinthic series. A third adherent genus, also labyrinthic, namely, *Polyphragma*, has been instituted by Von Reuss for a set of thin-shelled, erect, columnar, coral-like forms found in the Cretaceous beds of Germany. This bears considerable *primâ facie* resemblance, both in contour and mode of growth, to the genus *Haliphysema*, Bowerbank, the Rhizopod nature of which, first suggested by Mr. Carter, seems now to be fairly established. If we accept von Reuss's view of *Polyphragma* as the labyrinthic columnar type of the *Lituolidea*, *Haliphysema* would take the corresponding place amongst the non-labyrinthic forms. But the question still remains whether either genus belongs strictly to this particular group.

The term *Haplophragmium* is in general use amongst continental rhizopodists for the nautiloid and crozier-shaped, non-labyrinthic, rough arenaceous species; indeed, it appears to have been used abroad almost indiscriminately for the Cretaceous *Lituolæ*. Lastly, there are the straight or arcuate uniserial forms with labyrinthic chambers. To these Prof. von Reuss has given the generic name *Haplostiche*, but of them we know little beyond what he has himself written in his description of its Cretaceous representatives.

[1] Vide *Cyclammina cancellata*, p. 62.

[2] *Reophax scorpiurus*, de Montfort, 1808, 'Conchyliologie Systématique,' vol. i, p. 330, 83e. genre.

[3] Soldani, 'Testaceographia,' vol. i, pt. 3, p. 239, pl. 162, fig. K. *Nodosaria* (*Dentalina*) *scorpiurus*, d'Orbigny, 1826, 'Ann. Sci. Nat.,' vol. vii, p. 255, No. 40.

[4] *Placopsilina cenomana*, d'Orbigny, 1850, 'Prodrome de Paléont.,' vol. ii, p. 185, No. 758, "Espèce contournée en crosse adhérente aux corps."

[5] 'Annals and Mag. Nat. Hist.,' 1877, Ser. 4, vol. xix, p. 201, pl. 13, figs. 1—5.

The adoption of the subordinate generic terms, quoted from various authors in the foregoing paragraphs, as the basis of an arrangement of the *Lituoline* group, is not to be regarded as an indication of any material alteration of the views I have expressed in many previous papers, both alone and in conjunction with my friends Professors W. K. Parker and T. Rupert Jones. On the contrary, every new discovery seems but to furnish a missing link in a chain already nearly continuous. But though it is certainly impossible to draw a sharp line at any point marking a distinct stage of differentiation, there is none the less a necessity for distinguishing by name the central forms of the principal terms of the series, and these are what must stand as "species." Under such circumstances, or perhaps under any, "genus" is little more than a term of convenience.

With this explanation I would suggest the following scheme for the arrangement of the Lituoline family. It is in part adopted from that proposed by Professor von Reuss. No new terms have been introduced, its object being to set in order and give definiteness so far as our present knowledge extends to generic names already more or less in use, and so to avoid the confusion of fresh terminology. That the distinctions are to some extent artificial may be freely admitted, but any other arrangement that suggests itself is open to the same objection.

General Characters.—EXTERIOR MORE OR LESS ROUGHLY ARENACEOUS; SEPTATION OF THE POLYTHALAMOUS FORMS RUDIMENTARY OR IMPERFECT.

A. Non-labyrinthic.

a. Adherent by its flat surface . . .	*Placopsilina*, d'Orb.
b. Adherent, columnar, attached at one end	*Haliphysema*, Bow. (?).
c. Free, uniserial, moniliform, never spiral	*Reophax*, Montfort.
d. Free, partially or entirely spiral, nautiloid or crozier-shaped . . .	*Haplophragmium*, Reuss.

B. Chamber-cavities subdivided or labyrinthic.

a. Adherent by its flat surface . . .	*Bdelloidina*, Carter.
b. Adherent, subcylindrical, columnar, attached at one end	*Polyphragma*, Reuss (?).
c. Free, uniserial, straight or arcuate, never spiral	*Haplostiche*, Reuss.
d. Free, partially or entirely spiral, nautiloid or crozier-shaped . . .	*Lituola*, Lamarck.

Genus—PLACOPSILINA, *d'Orbigny*.

General characters.—Test adherent; composed of a single convex, tent-like chamber, or of many such segments vari-

ously combined. Polythalamous forms spiral, crozier-shaped, acervuline or linear in contour. Texture more or less roughly arenaceous.

PLACOPSILINA VESICULARIS, *n. sp.* Pl. V, fig. 2.

Characters.—Test, irregular in shape and size, spreading in indefinite patches over stones; usually composed of several convex chambers, either connected by short stoloniferous passages or crowded one against the other; margins rounded or lobulate, with simple or forked tubular extensions which form the pseudopodial apertures.

The drawing (Pl. V, fig. 2), scarcely needs verbal comment beyond the descriptive characters above detailed. *Placopsilina vesicularis*, is by no means a common species. In one of the "Porcupine" dredgings from the North Atlantic (1215 fathoms), sent to me by Sir Wyville Thomson, a number of the little stones brought up had adherent specimens in various stages of development, and from one of these the figure is taken.

Genus—REOPHAX, *de Montfort.*

General characters.—Test free, uniserial; consisting of a single flask-shaped chamber, or of a number of segments joined end to end in a straight, curved, or irregular line. Texture arenaceous, more or less rough externally; chamber cavities simple, non-labyrinthic. Aperture terminal, simple.

REOPHAX DIFFLUGIFORMIS, *n. sp.* Pl. IV, fig. 3, *a*, *b*.

Characters.—Test free, consisting of a single, undivided, rounded, or oval chamber, with produced neck. Wall thin, arenaceous; the constituent particles of sand neatly joined, and presenting a nearly smooth exterior. Length $\frac{1}{20}$ inch (0·5 millim.).

Had this little organism been found in fresh or brackish water, or even in shore-pools, it would, without doubt, have been assigned to the *Difflugiæ;* and it is perhaps an assumption rather than an ascertained fact that Rhizopoda with lobulate pseudopodia have no home in the deep sea. Nevertheless, as the test bears the same sort of relation to the moniliform *Lituolæ* as that of *Lagena* does to the *Nodosariæ*, there is a natural place for it in the Reticularian series.

There is nothing, either in the specimens themselves or in the forms with which they are associated, to suggest that they are other than mature representatives of a species; but the

minute structure of the test is identical with that of some varieties of *Reophax;* and in the absence of any distinguishing character, save the completion of growth in a single chamber instead of running on to form several segments, I am not disposed to create a fresh genus for its reception. It may be objected that the *Lagenæ* have been separated generically from the *Nodosariæ* on the ground of the monothalamous and polythalamous conditions of their respective tests. Without stopping to debate the propriety of this division from a strictly zoological point of view, two pleas may be urged in favour of it; firstly, that amongst the *Lagenæ* there are many varieties of surface ornamentation quite unknown in the Nodosarian series, which is strong evidence against the former being merely an arrested condition of the latter; and, secondly, the convenience of generic subdivision where there are so large a number of forms to be named and arranged. Neither of these reasons are applicable to the present case.

Amongst the hyaline Foraminifera only two globular or subglobular monothalamous types are recognised—*Lagena* and *Orbulina;* but amongst the *Arenacea* the simple spheroidal forms pertain to at least four or five genera, the most important of which are *Psammosphæra, Saccammina, Hormosina,* and *Reophax.* With the doubtful exception of *Psammosphæra,* all of these have polythalamous as well as monothalamous species.

The minute size of *Reophax difflugiformis,* its flask-like contour, and peculiar shell texture, are sufficient for its identification.

It appears to be essentially a deep-sea species, but of wide geographical distribution. I have note of its occurrence at five of the "Challenger" stations, of which one is in the North Atlantic, two are in the South Atlantic, and two in the South Pacific. In one of these the depth is 1900 fathoms, the other four vary from 2200 to 2740 fathoms.

Reophax nodulosa, *n. sp.* Pl. IV, figs. 7, 8.

Characters.—Test long, slender, tapering, straight or arcuate; consisting of several (usually less than twelve) segments, joined regularly end to end, and more or less embracing. Segments oblong, rounded, somewhat inflated, increasing in size from the first to the latest formed. Exterior more or less rough; interior neatly finished. Size very variable—sometimes as much as an inch (25 millim.) in length.

Foraminifera of a great variety of size and contour are embraced under this one specific name. Between straight and arcuate specimens no line can be drawn; again, some individuals are stout and few-chambered, each fresh segment being considerably larger than the previous one, whilst others have many chambers, are thin, and taper very gradually; some specimens are rough and sandy externally, whilst others are nearly smooth, the sand-grains being almost completely incorporated by the cement. In size the variation is correspondingly wide; minute specimens measure but half a millimètre, whilst large ones sometimes attain fifty times that length. The area of distribution is very wide; the finest specimens have been found at stations in the South Atlantic and in the North and South Pacific Oceans, at depths of from 1400 to 2000 fathoms.

REOPHAX MEMBRANACEA, *n. sp.* Pl. IV, fig. 9.

Characters.—Test long, slender, tapering, arcuate, or nearly straight; consisting of several (five to ten) subcylindrical or elliptical segments joined end to end. Walls thin, chitinous, beset with minute, adherent sand-grains; often transversely wrinkled. Length $\frac{1}{18}$ in inch (1·4 millim.).

It has long been known that, within certain limits, the composition of the investment of the testaceous Rhizopoda depends upon what may be termed accidental circumstances—conditions, namely, such as the degree of salinity of the water, its depth, the nature of the bottom, and similar extraneous influences. Illustrations of this fact have already been adduced from the genera *Miliola* and *Trochammina*. The former of these has normally a compact calcareous shell of porcellanous texture, the latter a smooth calcareo-arenaceous test; but both of them by degrees lose their calcareous nature in water holding a deficiency of inorganic salts in solution, as in brackish pools and river estuaries, and become chitinous or chitino-arenaceous.

In one or two deep soundings from a very muddy bottom minute moniliform *Lituolæ* have been found with a delicate investment of light brown tint and nearly transparent. The test is very thin, and is only partially soluble in weak acids; it appears to consist of calcareous and chitinous matter, with sometimes a few very minute adherent or embedded siliceous sand-grains. The mineral constituents exist in sufficient quantity to effervesce slightly with an acid, and to render the test brittle rather than flexible after it is dried; but the surface is wrinkled transversely, in a manner strongly sug-

gestive of a membrane covering a soft or plastic mass. Unfortunately the species is very rare, and the specimens exceedingly small, so that material does not exist for any close investigation as to the chemical nature of the test, nor is sufficient known of the condition of the sea bottom, in these cases, to account for the deviations from the normal type of structure.

The best examples hitherto procured of *R. membranacea* are from 1900 fathoms, off the coast of South America, in about the same latitude as Buenos Ayres.

REOPHAX SPICULIFERA, *n. sp.* Pl. IV, figs. 10, 11.

Characters.—Test elongate, straight or arcuate; consisting of a few (three to six) cylindrical segments. Shell-wall composed of siliceous spicula arranged side by side, and firmly cemented together. Spicula often protruding more or less from the base of the segments. Length $\frac{1}{25}$ inch (1·0 millim.).

This is one of the many species of Foraminifera that give evidence of considerable selective power in respect to the material employed for the construction of their tests. That it is selective power, and does not depend upon the absence of the angular sand-grains, which are the ordinary constituent of the composite shells of the *Lituolæ*, is rendered pretty certain by the fact that other species occur in the same soundings in their normal sandy condition. Again, the orderly arrangement of the spicula side by side and the neat and compact masonry of the walls cannot be accidental, contrasting strongly as it does with the indiscriminate use of sponge-spicula amongst sand-grains and various other extraneous bodies, seen in the tests of the rough Lituoline forms.

Reophax spiculifera is, comparatively speaking, a minute species, being seldom more than $\frac{1}{25}$ inch (1 millim.) in length. It occurs at several of the "Challenger" stations in the South Pacific, at depths varying from 250 to 2300 fathoms, generally on muddy bottoms.

Genus—TROCHAMMINA, *Parker and Jones.*

The genus *Trochammina* was established by Messrs. Parker and Jones,[1] for a group of arenaceous Foraminifera characterised primarily by their thin, smooth, finely-cemented tests. Although the name was originally applied to a Rotali-

[1] 'Annals and Mag. Nat. Hist.,' 1859, ser. 3, vol. iv, p. 347.

form shell,[1] the authors prefer to regard the trochoid, often adherent variety (*Tr. squamata*, J. and P.), as the type of the genus. The tenuity and fine texture of the arenaceous investment rather than the mere general contour has very properly been accepted as the essential distinction, and fresh forms possessing this character have one by one been added to the genus until it has come to include a series having a very wide range of morphological variation. Not only have we trochoid and Rotaliform, but nautiloid, Milioline, Spirilline and, as we shall presently see, Lageniform and Nodosarian modifications of the type. In addition to these there are certain simple adherent organisms, described by d'Orbigny under the name *Webbina*,[2] whose natural affinity is with the same group; in point of fact the term *Trochammina*, with these repeated additions, has come to comprehend an assemblage of forms having the dimensions of a Family rather than a genus. The series is now altogether too bulky and diverse to be zoologically convenient, and it is necessary to consider whether it may not be subdivided with advantage. Prof. von Reuss makes a distinct genus of the Spirilline non-septate forms, to which he gives the name *Ammodiscus*, and this term has been generally adopted by German authors. If we accept *Webbina* to distinguish the simpler adherent varieties and *Ammodiscus* for the free, non-septate forms, and limit the application of *Trochammina* to the well differentiated septate modifications of the type, to which it was first applied, there only remain the *Nodosaria*-like species to be provided for, and for these the term *Hormosina*[3] would be a suitable, generic or subgeneric appellation. I venture, therefore, to propose the following arrangement of the group.

It must be borne in mind, however, that the allusions which have been made to the minute structure of the test apply only to specimens existing under normal conditions, *i.e.* in sea water of ordinary salinity. I have elsewhere shown[4] that if the proportion of mineral constituents is from any cause reduced, as in river estuaries and brackish pools, the arenaceous investment of the *Trochamminæ* becomes less calcareous, and specimens may sometimes be found under such circumstances, which are scarcely altered by treatment with acids. Such individuals are still sandy and preserve to

[1] *Nautilus inflatus*, Montagu, 1808, 'Test. Brit. Suppl.' p. 81, pl. 18, fig. 3.—*Rotalina inflata*, Williamson, 1858, 'Rec. For. Gt. Br.,' p. 50, pl. 4, fig. 93, 94.

[2] 'Foram. Canaries,' p. 125.

[3] From ὅρμος, a necklace.

[4] 'Ann. and Mag. Nat. Hist.,' ser. 4, vol. vi, p. 38, 51, &c., pl. 11 fig. 5, *a*—*c*.

a great degree their ordinary form and appearance, but the finely cemented test is replaced by a membranous or chitinous envelope, to which the sand-grains are adherent, or in which they are partially embedded.

TROCHAMMINA.

General characters.—Test thin; composed of minute sand-grains incorporated by calcareous or other inorganic cement of fine texture, or embedded in a chitinous membrane; exterior smooth, often polished; interior smooth or rarely reticulated, never labyrinthic.

Ammodiscus, *Reuss.*—Test free, formed of a tube of nearly even diameter coiled upon itself in various ways; sometimes slightly constricted at intervals, never really septate.

Examples: *Ammodiscus incerta* (d'Orb.); *A. gordialis*, J. and P.; *A. charoides*, P. and J.; *A. milioloides*, P., J., and K.; *A. pusilla* (Geinitz); *A. filum* (Schmid); &c.

Trochammina, P. and J. (proper).—Test rotaliform, nautiloid or trochoid, free or rarely adherent, more or less distinctly septate.

Examples: *Trochammina inflata* (Mont.); *Tr. coronata*, nov.; *Tr. squamata*, J. and P.; *Tr. macrescens*, Brady; *Tr. trullissata*, nov.; *Tr. ringens*, nov.; *Tr. pauciloculata*, nov.; &c.

Hormosina, *nov.*—Test consisting typically of several segments in a single straight or arcuate series. When the primordial segment is large, growth is arrested and a lageniform test is the result.

Examples: *Hormosina globulifera*, nov.; *H. ovata*, nov.; &c.

Webbina, *d'Orbigny.*—Test partially or entirely adherent; consisting of a single hemispherical, oval, or subspherical chamber, with or without an adherent semi-cylindrical neck; or of a series of tent-like chambers united by adherent stoloniferous tubes.

Examples: *Webbina irregularis*, d'Orb.; *W. hemispherica*, P., J., and B.; *W. alternans*, P. and J.; *W. clavata*, P. and J.; &c.

Trochammina trullissata, *n. sp.* Pl. V, figs. 10, *a b*, 11.

Characters.—Test nautiloid, compressed, lenticular, somewhat excavated at the umbilicus; composed of about three convolutions, of which but little more than the latest is visible; peripheral margin acute or somewhat

rounded. Segments about nine in each convolution. Septa marked by more or less sinuate lines, only slightly depressed. Exterior smooth, usually polished; interior surface often reticulate; colour brown. Aperture crescentic, situate on the face of the terminal chamber, close to the margin of the previous convolution. Diameter $\frac{1}{20}$ inch (1·25 mm).

The first examples of this beautiful little shell that came under my notice were in the Rev. A. M. Norman's mountings from the "Valorous" dredgings in Davis' Straits, but the "Challenger" material has yielded a supply of specimens from a number of localities. *Trochammina trullissata* is easily distinguished from any other species by its perfectly regular, nautiloid, or Nonionine contour, the number of chambers in each whorl, their sigmoid sutural lines, and its polished brown exterior. It is not unlike the very large nautiloid type, *Cyclammina*, in its general conformation, but differs widely from it in point of size and internal structure. The inner surface of the test of *Tr. trullissata* sometimes exhibits a slightly raised reticulation, but this in no case, so far as my observation goes, is more than a mere superficial marking, and never comes to anything resembling the cancellated shelly growths that often nearly fill the chambers of *Cyclammina*.

The distribution of the species is wide, but it is by no means abundant in any locality. The best "Challenger" specimens are from two stations in the North Atlantic and two in the South Atlantic, the depth of water varying from 390 to 2200 fathoms.

TROCHAMMINA RINGENS, *n. sp.*[1] Pl. V, fig. 12, *a*, *b*.

Characters.—Test nautiloid, oblong, compressed, biconvex; composed of few convolutions, of which the last entirely encloses the previous ones. Peripheral margin acute-angular, or slightly rounded, lobulate; septal lines curved, somewhat excavated. Segments large, about five in each convolution, embracing. Colour brown, surface usually polished. Aperture an arcuate slit, overhung by a slight swelling or prominence on the face of the terminal chamber, and near the margin of the previous convolution. Longer diameter $\frac{1}{20}$ inch (1·25 mm.).

[1] This form was recorded by Mr. Norman, in the "Valorous" Report ('Proc. Royal Soc.,' xxv, 1876, p. 213), as "very near to, if not identical with, *Globigerina arenaria*, Karrer," but he has subsequently received types of that species from Dr. Karrer, and is now satisfied of their entire distinctness.

Trochammina ringens is nearly allied to the species last described; the points of distinction, are nevertheless sufficiently apparent. Compared with *Tr. trullissata*, it has only about half the number of segments in each convolution, and the final whorl completely encloses the previous ones, instead of leaving the penultimate coil partly exposed at the centre. The general contour of the test is biconvex rather than depressed in the umbilical region, and the terminal segment is conspicuously large. In colour, texture, and minute structure, the two forms are alike, but *Tr. ringens* has none of the reticulation of the inner surface of the shell that has been ascribed to *Tr. trullissata*.

It appears to be a very rare species. I have only notes of its occurrence in three of the "Challenger" dredgings, one of them from the North Atlantic, off Siera Leone (1750 fathoms), one from the South Atlantic, off Buenos Ayres (1900 fathoms), and the other from the North Pacific (1850 fathoms).

Since the above description was written I find that the Rev. A. M. Norman has this form also in his collection from the "Valorous" dredgings at the entrance of Davis' Strait, in 1750 fathoms.

TROCHAMMINA PAUCILOCULATA, *n. sp.* Pl. V, figs. 13, 14.

Characters.—Test ovoid, slightly compressed, obscurely spiral; composed of about two convolutions, the latter of which almost entirely conceals the earlier one. Segments few, usually three in each convolution, inflated; sutures slightly constricted. Test thin, finely arenaceous, brown; exterior smooth, often polished; interior smooth. Aperture a curved slit on the superior surface, at the inner margin of the last segment. Length, $\frac{1}{60}$ inch (0·45 millim.).

Though a very minute species *Troehammina pauciloculata* is striking and distinct. It is isomorphous with the genus *Allomorphina* of Reuss, the recent specimens of which are of even smaller dimensions, but it has the shell texture characteristic of its own genus, whilst Reuss's type is hyaline and perforate. In its general plan of growth it closely resembles the Rotalians, notwithstanding its small number of segments, and their unsymmetrical disposition.

TROCHAMMINA CORONATA, *n. sp.* Pl. V, fig. 15.

Characters.—Test nautiloid, biconcave, composed of few convolutions; peripheral margin lobulate and rounded. Segments distinct, variable in number, inflated. Aperture

simple, situate on the face of the terminal segment near its junction with the previous convolution. Colour buff to reddish brown; surface smooth, not polished. Diameter $\frac{1}{10}$ inch (2·5 mm.).

This handsome species differs from its congeners in size as well as in general contour. The larger specimens are fully one tenth of an inch in diameter, and are coronate or biconcave in form. The chambers are few in number, tent-like, and more or less embracing, though the successive convolutions do not entirely conceal those immediately preceding them. The width of the spiral band increases with each turn, and the chambers of the final whorl are very much larger than those of the earlier ones. The texture of the test is uniformly very finely arenaceous and opaque, but within certain limits, *i.e.* from a creamy white to a dark brown, the colour varies a good deal. Amongst previously described Foraminifera it is not easy to find any with characters approaching those of *Trochammina coronata*; perhaps the nearest is *Tr. inflata*, but in that species the test is Rotaliform, in other words, all the segments are more or less exposed in a spiral line on the superior face, whilst those of the last convolution only are visible on the inferior side, which is very different from the symmetrical, nautiloid habit of the new species.

Fine specimens of *Tr. coronata* have been met with at the western side of both the North and South Atlantic, namely, at two stations near the West Indies (390 fathoms and 450 fathoms), and at two stations off the coast of South of America (675 fathoms and 1900 fathoms).

TROCHAMMINA LITUIFORMIS, *n. sp.* Pl. V, fig. 16.

Characters.—Test free, crozier-shaped; consisting of an irregularly septate or pseudo-septate tube, spiral at its commencement, afterwards linear. Segments irregular in size, subcylindrical or ventricose; sutural lines excavated. Aperture simple, terminal. Surface smooth; colour light brown. Length $\frac{1}{7}$ inch (3·7 millim.).

There are already known at least two crozier-shaped varieties of *Trochammina*, the Carboniferous *Tr. centrifuga*, and the Permian *Tr. filum*, but these are alike characterised by the absence of septa both in the spiral and linear portions of the tests, and pertain rather to the *Ammodiscus* series than to *Trochammina* proper. They are also, both of them, comparatively minute in size. The specimens now described are of fine dimensions, though somewhat irregular in genera

contour and in septation. In colour and shell-texture they are precisely similar to *Trochammina coronata*.

Trochammina lituiformis has been met with in the North Atlantic (West Indies, 390 fathoms, and off the Azores, 900 fathoms), and at two stations in the South Atlantic, on the coast of South America in about the latitude of Pernambuco (350 and 675 fathoms).

HORMOSINA GLOBULIFERA, *n. sp.* Pl. IV, figs. 4, 5.

Characters.—Test composed of a single spherical chamber with a tubular neck, or of several (2 to 6) such chambers, each larger than its predecessor and more or less embracing it. Segments arranged in a straight or curved linear series, terminating in a thin tubular neck. Texture very finely arenaceous, surface smooth. Length of polythalamous specimens often $\frac{1}{8}$ inch (3 millim.).

The figures, 4 and 5 of Pl. IV, afford a very insufficient representation of this species, inasmuch as specimens are not unfrequently found possessing four, five, or even more chambers, and of correspondingly increased dimensions. In default of room for sufficient figures, the object has been to illustrate a tendency not uncommon amongst Foraminifera, which shows itself strikingly in this particular species, namely, the cessation of growth after the formation of a chamber of relatively large size. As a rule the specimens of *Hormosina globulifera* which have the largest number of segments are those with the smallest initial chambers, and, on the other hand, if a very large primordial chamber is found the test usually remains monothalamous and no further growth takes place. A comparison of the size of the Lageniform test (fig. 4) with that of the earlier segment of fig. 5, will illustrate this fact. The rule holds good not only of the first chamber, but in varying degree to the life-history of Foraminifera generally. It is very commonly seen in polythalamous species that, with the formation of a chamber of abnormal size, the growth, that is, the continued segmentation of sarcode, is abruptly stopped. Instances of this occur in every section of the Order. Whatever, therefore, may be the significance of monothalamous as distinct from polythalamous tests amongst the Rhizopoda of other groups, the character in this case is not of specific, still less of generic importance.

There is no difficulty in distinguishing these *Hormosinæ* from their Lituoline isomorphs by their regularity and

symmetry of form, their thin walls, and smooth, almost homogeneous, tests.

H. globulifera is essentially a deep-water Foraminifer. Out of eight localities in which I have notes of its occurrence, six are at depths of more than 1000 fathoms, and three of these at more than 2000 fathoms. Its distribution appears to be world wide, the "Challenger" collections furnishing specimens from both the North and South Atlantic and the North and South Pacific Oceans.

HORMOSINA OVICULA, *n. sp.* Pl. IV, fig. 6.

Characters.—Test long and very slender, tapering; composed of several fusiform segments joined end to end, without overlapping, in straight or slightly curved linear series. Walls thin, texture very finely arenaceous. Colour yellowish brown, with a band of somewhat darker hue encircling the narrowest part of the stoloniferous tubes. Length, $\frac{1}{5}$ inch (5 millim.).

A very delicate fragile little organism and one seldom found entire. *Hormosina ovicula* stands in much the same relation to *H. globulifera* that *Nodosaria pyrula* does to *N. radicula*; that is to say, its segments are produced at the two ends and are joined by their narrow extremities, instead of the successive lobes being sessile and more or less embracing. The deepening of the brown colour in portions of the test, which has been noticed in connection with other species, shews itself in the present instance in the little ring surrounding the stoloniferous tubes at their narrowest point. Each of these points having been of course, in its turn, the pseudopodial aperture of the shell.

Hormosina ovicula is, to even a greater degree than its congener, *H. globulifera*, a deep-water species. Specimens have been met with in six of the "Challenger" dredgings, which represent depths ranging from 1900 to 2600 fathoms, and I have no note of its occurrence in shallower water. Of these, two were dredgings from the South Atlantic, two from points lying to the South of Australia, and two from the North Pacific.

Genus—CYCLAMMINA, *nov.*

(κύκλος, a circle; ἄμμος, sand.)

CYCLAMMINA CANCELLATA, *n. sp.*

Nautiloid *Lituola*, Carpenter, 1875. 'The Microscope and its Revelations,' fifth ed., p. 536, fig. 274, *a*, *b*, *c*.
Cyclammina cancellata (Brady, M.S.), Norman, 1876. 'Proc. Roy. Soc. Lond.,' vol. xxv, p. 214.
Lituola canariensis, Carter, 1877. 'Ann. and Mag. Nat. Hist.,' ser. 4, vol. xix, p. 203, pl. 13, figs. 26—29.

Characters.—Test free, nautiloid, biconvex, depressed at the umbilicus; margin entire or slightly lobulate, angular or somewhat rounded; composed of from two to three convolutions, each of which encloses completely, or almost completely, the previous ones. Segments numerous, ten to sixteen in the last convolution; narrow, bounded by sinuate, slightly excavated lines radiating from the umbilicus. Interior of the chambers almost (sometimes entirely) filled with finely arenaceous tubular growths. Surface smooth and imperforate, except where abraded; colour, various shades of brown. Aperture normally a crescentic slit in the terminal segment, close to its union with the previous convolution; but, in addition, there are often a number of large pores irregularly distributed on the face of the terminal chamber. Size variable; many specimens reach $\frac{1}{6}$ inch (4 millim.) in diameter.

The main structural features of this interesting type have been already treated by Dr. Carpenter (loc. cit.); but as the manuscript name appended to my specimens several years ago has been employed by at least one author to distinguish the species, it seems right that I should summarise its zoological characters. This is the more necessary because the organism has no place in the scheme which I have suggested for the Lituoline genera. I cannot quite agree with Dr. Carpenter in regarding it as a *Lituola;* still less with Mr. Carter in assigning it to *Lituola canariensis*, which is a very distinct, minute, thin-shelled, *Nonionina*-like species. As I believe it is one of the forms concerning which we have more to expect from Dr. Carpenter's pen, it would be unbecoming in me to enter into minute details respecting its structure.

Cyclammina cancellata is very widely distributed. In

addition to the examples from North Atlantic localities, obtained by the scientific staffs of the "Porcupine" and the "Valorous," fine specimens have been found in many of the "Challenger" dredgings, namely, from off the Canaries and from the West Indies; from two or three stations in the South Atlantic; from the South Pacific (off New Zealand); and from the Eastern Achipelago. The depths of these soundings range from 350 fathoms to 1900 fathoms, but the largest specimens occur on bottoms of less than 700 fathoms.

A very interesting modification of the type—perhaps only a variety—occurs in deep water off the coast of South America. It is somewhat smaller than the common form, and differs from it in general contour and in colour. Its shape is nearly globular, so that it may be regarded as an isomorph of *Nonionina pompilioides;* it is of a beautiful grey hue, and the surface presents almost more than the normal glossiness.

Researches *on the* Flagellate Infusoria *and* Allied Organisms. By O. Bütschli, Professor of Zoology in the University of Heidelberg.[1]

Professor Bütschli points out the value of a careful study of the Flagellata, some of which appear to be more nearly allied to the vegetable than to the animal kingdom. He concludes his preface with a hope that he may be able at a future time to amplify the present record.

I.—The True Flagellata.

Spumella.—Cienkowski ("Ueber Palmellaceen und einige Flagellaten," 'Arch. für mikr. Anat.,' Bd. vi, 1871, p. 432).

Small Flagellata, which, so far as is known, are colourless. They are either free-swimming, or are temporarily attached by a threadlike prolongation of the hinder end of the body.

[1] Abridged from a paper in the 'Zeitschrift f. Wissensch. Zoologie,' Bd. xxx, by D'Arcy Power, B.A., Exeter Coll., Oxford.

Anteriorly is a flagellum of considerable size, near which are sometimes one or two smaller accessory flagella. Food materials are received into a vacuole formed at the base of the flagellum ; this vacuole in some forms becomes converted into a liplike prominence. A nucleus is present. Reproduction has as yet only been seen to take place by simple division during the motile stage. According to Cienkowski a cyst is produced in the inner part of the protoplasmic body of the organism, a portion of which is consequently lost by the encystation.

Spumella termo, J. Clark ('Ann. and Magaz. Nat. Hist.,' 4th ser., vol. i, p. 135, figs. 1—4).

Monas termo, Ehrenberg (?), ('Die Infusionsthiere als vollkommene organismen,' Leipzig, 1838, p. 7, pl. i, fig. 2.)

These Monads (Plate vi, figs. 1 and 2) were often found by Bütschli as small Flagellata widely diffused in foul water. In spite of a few minor differences they appear to be identical with the form described by Clark, and with the *Monas termo* of Ehrenberg. *Spumella termo* is a small organism with a somewhat oval and flattened body ; the greatest thickness is 0·005—0·006 mm. in an average-sized specimen. These small Flagellata are usually more or less fixed by the hinder end of the body, which is not rounded off, although no peculiar shell-like prolongations of this end, produced from the body itself, are visible ; but occasionally, as generally happens in *Spumella vulgaris* (Cienk.), the posterior end is drawn out into a delicate process. Sometimes the Spumella leaves its resting place and swims about rapidly by means of its flagellum. During the resting stage the flagellum, which springs from the anterior end of the body, is seen curved in the way figured.

No accessory flagellum is perceptible in this species. Near the base of the flagellum rises the lip as a corner of the somewhat sharply defined anterior edge of the body. The lip either consists of colourless protoplasm, like the true body of the organism, or it appears more transparent, because it has produced within itself a vacuole filled with fluid (fig. 1 a). This vacuole of the liplike prominence is subservient to the reception of food ; thus, the Bacteria and Micrococci, which constitute the chief food of the organism, are driven against the liplike prominence by the lashings of the flagellum ; they either escape or are taken into the vacuole, which is now much swollen (fig. 1 b). The vacuole then passes gradually down, along the side of the body

(fig. 1 c), to the posterior end, where it ultimately becomes so entirely surrounded that it no longer projects sac-like beyond the body. After a time such particles appear to lose the vacuole by which they were surrounded, and numbers are found lying free in the protoplasm. Occasionally, also, vacuoles containing no food materials are carried backwards. It thus seems as if the vacuoles were formed at definite intervals, and were pushed back without the ingestion of food acting as a necessary stimulus. The vacuoles may also be formed directly on the ingestion of food, although one is usually readily prepared for such an event in the liplike prominence. Clark supposed that there was a cytostome or cell mouth between the base of the flagellum and the lip, usually kept closed, which allowed the lip to play a part in the swallowing of food. The process of the rejection of food remnants has been observed by Bütschli in a stalked form of moderate size; the materials to be extruded were surrounded by large irregular vacuoles formed from time to time within the body; these vacuoles were moved to the side on which was the lip, and stood out hernial like from it, when they either emptied their contents, or, still retaining them, were pinched off from the body.

A single rapidly contracting vacuole was constantly present on the side opposite the lip. A vesicular nucleus with clear border and distinct nucleoli was frequently visible in the anterior part of the body, not far behind the base of the flagellum.

Of the phenomena of reproduction, Bütschli only succeeded in observing the frequent divisions, which are executed in a way which seems to be general in the small proportion of Flagellata which have as yet been examined in regard to this point (Plate vi, fig. 2). In the individual which is about to divide a second flagellum makes its appearance. Thus instead of the primitively simple flagellum, two are formed. The shape of the organism, however, is not noticeably changed, except that it appears slightly more globular, and the lip prominence seems to pass away. The further process of division can be followed in fig. 2, a to e. The body of the organism is first constricted and then divided between the separated flagella. The pinched-off parts then gradually draw away from each other for a considerable distance, till the two daughter organisms are only united by a very delicate thread, which ultimately breaks, and the two products of the division separate from each other. The mode in which the multiplication of the flagella takes place is not determined. The entire process of division

occupies only a few minutes, but from the minuteness of the organism the behaviour of the nucleus cannot be observed. No encystation has as yet been noticed in this form.

Spumella neglecta, *Monas neglecta*, cf. Clark (loc. cit., p. 138, pl. v, figs. 5, 6), is closely allied to the form just described.

Spumella vulgaris, Cienkowski (loc. cit.). Bütschli is able on the whole to confirm Cienkowski's description. It is distinguishable from *Spumella termo* by its very round, and almost spherical shape, and by the absence of the liplike prominence.

Spumella (?) truncata, Fresenius ("Beiträge zur Kenntniss kleinster organismen," 'Abhandl. der Senkenberg. Gesselsch. zu Frankfurt-a-M.,' Bd. ii, pl x, fig. 42), is placed provisionally with Cienkowski's Spumella; it is a very characteristic organism, and has been well figured by Fresenius, who has described it as *Monas truncata* in the explanation of his plate, though he has omitted all mention of it in the text. The organism (Plate vi, fig. 3) is very flat, being but thin in proportion to its length and breadth. The contour of the broad side is somewhat oval, although the end bearing the flagellum is cut off to form a sharp slope; the opposite pole, on the other hand, being either smoothly rounded off or moderately pointed. From the higher portion of the anterior end of the body—the sloping portion—proceed two flagella, which are of no great length. In the clear protoplasmic body, near the longer side, is a vesicular nucleus with large dark inner body, which is generally somewhat in front of the centre of the body. The contractile vacuole is on the opposite and shorter side of the body, close to the front anterior border. Immediately in front of the vacuole is a dark band, running nearly parallel to the oblique anterior border, from the shorter side almost to the base of the flagellum. This band is composed of a substance of high refractive index, which on closer scrutiny always appears to be irregularly granular; and it is sometimes quite apparent that it is made up of a number of highly refracting granules. This band is analogous with the one found by Cienkowski in *Spumella vulgaris*, and should perhaps be classed with the so-called eyespots in other Flagellata.

The protoplasmic body contains great numbers of permanent vacuoles, amongst which the food vacuoles, with their enclosed particles, are so clearly distinguishable that there

is no doubt that *Spumella truncata* takes solid food, although neither the kind of nutriment nor the mode of ingestion is yet ascertained, owing to the rapid and uninterrupted movements of the organism.

Chromulina Cienkowski ("Ueber Palmellaceen und einige Flagellaten," 'Archiv. für Mikr. Anat.,' Bd. vi, 1871, p. 435).

Small Flagellata with a flagellum, contractile vacuole, and coloured disc. Inside is a cyst—the entocyst. No solid food appears to be taken. The presence of the nucleus is doubtful.

Chromulina ochracea, Ehrenberg ('Die Infusionsthiere als Vollkommene organismen,' Leipzig, 1838, p. 11, pl. i, fig. 7), *Monas ochracea*, Ehrb.—These small organisms are placed in the genus *Chromulina, Cienk.*, in spite of the fact that the production of a cyst within the protoplasmic body—which is the most remarkable peculiarity of the species—has not yet been observed. The identity with *Monas ochracea* of Ehrenberg is very doubtful.

Chromulina ochracea (Plate vi, fig. 4) is a small organism measuring 0·006 to 0·008 mm. in length and breadth; it was obtained in the lake in the Grand-ducal park at Carlsruhe, where it was present in such numbers as to tinge the water of a yellowish-brown colour. The body is much flattened (fig. 4 c, seen from the narrow side), being heart-shaped, oval, or sometimes irregular in appearance, when looked at from the flat side (fig. 4 a b). Within the colourless protoplasm composing the body, two large coloured discs of a brown or yellowish-brown colour are constantly present; these discs entirely fill up the interior of the body. In the narrower end of the body lies a deep red eyespot of elongated rod-like appearance, and close to it are usually a number of dark granules of high refractive index (fig. 4 a and b). About the centre of the body is a contractile vacuole, which is very conspicuous during the diastole, and which contracts tolerably slowly. The very rapid flickering, as well as convulsive and tottering movement, which is only broken at intervals by short periods of rest, is due to a flagellum of two or three times the length of the body, which is very difficult to observe. It probably arises, not from one end of the body, but from one of the broad surfaces of the body (fig. 4 c). No nucleus has yet been noticed. Occasionally some of the organisms which seem to have lost their flagellum, execute amœboid movements and put out tolerably long pseudopodia.

The author next describes a small parasitic Flagellate found in the alimentary canal of a free living Nematode *Trilobus gracilis*. The individuals were aggregated together by their non-flagellate poles, into radiating colonies. Single individuals, which are easily isolated, are very long and spindle-shaped, so as to be almost rod-like (from about 0·011 mm. in length); they are colourless, and are provided at the blunter end of the body with a large thick flagellum, of almost twice the length of the body. A contractile vacuole lies somewhat behind the base of the tentacle, and at some distance below this, in the otherwise feebly and very finely granular protoplasm of the body, is seen a small mass of high refractive index, composed of dark granules. No nucleus is observable. The movement of the organism is tolerably slow after it has been removed from the intestine of Trilobus, at least in water, in which it dies rather quickly.

Antophysa, Bory de Vincent.

Small colourless Flagellata forming racemose colonies; the number of individuals forming a colony varies from two to fifty, according to Clark. The individuals of each racemose colony are attached without lateral connection, by a short stalk-like prolongation of the hinder end of the body to a fine terminal branch of the thick, branching, brown-coloured main stem; each individual has a large flagellum and a delicate accessory flagellum, a lip-like prolongation for the ingestion of food, and a contractile vacuole. The nucleus is doubtful. Reproduction by fission on the stalk in the colony; whole colonies, as well as single individuals, frequently separate themselves and swim about, such individuals again becoming fixed, probably form the commencement of a new colony.

Antophysa vegetans, O. F. Muller.

Volvox vegetans, Muller ('Animalcula Infusoria,' p. 22, pl. iii, figs. 22—25).

Antophysis Mülleri, Bory ('Encyclopéd. méth.,' 1824; 'Hist. Nat. des Zoophytes,' p. 66).

Epistylis vegetans?, Ehrb. ('Die Infusionsthiere als vollkommene organismen,' Leipzig, 1838, p. 285, pl. xxvii, fig. 5).

Antophysa Mülleri, Dujardin ('Histoire nat. des Infusoires,' Paris, 1841, p. 302).

Antophysa Mülleri, Cohn ('Entwickelungsgeschichte der Mikroskopischen Algen und Pilze, Nov. act. Ac. c. L.C., &c.,' Bd. xxiv, p. 109, pl. xv, figs. 1—8).

Antophysa Mülleri, Clap. and Lachm (Claparède and Lachman, 'Études sur les Infusoires,' pp. 64—66).

Antophysa Mülleri, Clark ('Ann. and Magaz. Nat. Hist.,' 4th ser., vol. i, p. 209).

Antophysa Mülleri, Archer ("On *Antophysa Mulleri*," this Journal, vol. vi, N. S., 1866, p. 182).

Antophysa Mülleri, Fromentel ('Études sur les Microzoaires,' Paris, p. 337, pl. xxvi, fig. 5).

These organisms (Plate vi, fig. 6) were discovered by O. F. Müller. Kuetzing supposed that the brown stalk was a peculiar fungus—Stereonema—and distinguished six different kinds. Lately (1861) Archer has shown that the main stem of the organism increases independently, and that the colonies at the terminal branches are to be looked upon as swarm spores, which are, from time to time, produced from the branches, so that the main stem is to be regarded as the chief organism. Dujardin, in opposition to Ehrenberg, was the first to prove adequately the flagellate nature of these organisms, which he placed near Ehrenberg's genus Uvella.

Bütschli now confirms Clark's account in its essential features. For instance, as regards the presence of a delicate, small, and very rapidly-vibrating accessory flagellum, close to the base of the chief flagellum, and as to the existance of a lip or beak-like prominence of similar nature with, and in the same position as, the one found in *Spumella termo*, Clark.

Reproduction takes place within the colony by fission of the individuals, as described by Clark (l. c.), although Bütschli states that he has seen nothing of the case or coat described by that author.

Division (Family ?): Cylicomastiges.

The two genera, Codosiga and Salpingœca, are closely allied outwardly. They differ chiefly, if not solely, in the fact that the latter are provided with peculiar shells, like Bicosœca and Dinobryon, whilst the former genus, on the contrary, is devoid of such shell. Both genera possess a remarkable peculiarity in the existence of a large collar or calyx surrounding the base of the single flagellum; and it appears right to make this point one of a classificatory importance. The endoderm cells of Sponges are, as Clark has shown, provided with a similar collar, and so, classify Sponges as one will, there still remains the remarkable agreement—still requiring explanation—between the flagellum-bearing cells of the Sponges and certain flagellate organisms. This appears the

more noteworthy, as this peculiar condition of the flagellate cells has never been found in other organisms.

Codosiga, Clark ('Ann. and Mag. Nat. Hist.,' 4th ser., vol. i, p. 191).
Antophysis, Bory ('Encycl. Méthod. Hist. Nat. des Zoophytes,' 1824).
Epistylis, Ehrb. ('Die Infusionsthiere als vollkommene organismen,' Leipzig, 1838).
? *Pycnobryon*, Fromentel ('Études sur les Microzoaires,' Paris, pp. 212 and 337).
Uvella, Fromentel, op. cit., p. 338.

Small, colourless, colony-forming Flagellata. The single individuals have a long flagellum anteriorly, arising within a very large collar. The organisms are naked, devoid of a covering. Food is ingested into a food vacuole situated outside the collar at its base. A contractile vacuole and nucleus are present. The colonies are formed as they are in Antophysa, the individuals arising from the end of a straight and unbranched main stem, which is frequently of considerable length. Reproduction by longitudinal fission of the individuals forming the colony has been observed.

Codosiga botrytis, Ehrb.
Antophysis solitaria, Bory ('Encyc. méth.,' p. 67).
,, ,, (Bory), Fresenius ("Beiträge zur Kenntniss kleinster organismen," 'Abhandl. der Senkenberg Gesellsh. zu Frankfurt-a-M.,' Bd. ii, p. 233, pl. x, fig. 29, 30).
Epistylis botrytis, Ehrb (p. 284, pl. xxvii, fig. 4).
Codosiga pulcherrima, Clark (loc. cit., p. 139, pl. v, figs. 7—27).
? *Uvella disjuncta*, Fromentel (p. 338, pl. xxv, fig. 8).
? *Pycnobryon socialis*, Fromentel (p. 137, pl. xxvi, fig. 9).

These very interesting, but yet common, forms (Pl. vi, fig. 7) were discovered in 1858 by G. Fresenius, who with reason held that they were the same as the *Epistylis botrytis* of Ehrenberg; whether, on the contrary, *Antophysa solitaria* of Bory de Vincent, after which Fresenius named the species, is identical with the *Epistylis botrytis* of Ehrenberg is doubtful. The number of organisms going to make up a colony was long a matter of dispute; usually only four or five are seen, whilst Clark has observed eight, and Ehrenberg ten. Solitary individuals are frequently mounted upon short slender stalks. The pedicels of older colonies, richer

in individuals, are thicker and longer (fig. 7 a); at their attached base a flattened portion serving for attachment is seen under favorable circumstances, whilst the stem itself appears tubular, dark sides, and a clear homogeneous axis substance being distinguishable. Occasionally the usually colourless stem is tinged of a somewhat yellowish brown.

The individuals forming the colony spring from the upper end of the stem, each being carried upon a delicate protoplasmic stalk, which passes directly into the hinder end of the organism. These stem-like prolongations of the hinder poles are not contractile, at least not in any noticeable degree. The flagellum springs from the centre of the obtuse anterior pole of the body. When it is at rest it frequently falls, somewhat curled in a very characteristic way. The delicate membrane-like collar surrounds the blunted anterior pole (fig. 7 a—c); it is usually seen in optical section as two dark diverging lines, which at first give the impression of two accessory flagella, and for these they have been occasionally mistaken.

Fresenius described the collar as a delicate, blunted appendage, from which a cilium causing motion (Bewegungsfaden) projected.

The size and appearance of the collar are exceedingly variable; sometimes it projects only very slightly beyond the anterior end. Separate specimens have been seen swimming freely, which did not possess any trace of a collar. Generally it is of considerable height, as in fig. 7 a, b, occasionally (fig. 7 c) it is a very noticeable object. Clark has observed that this change in the height of the collar is very rapidly executed in one and the same individual, that the funnel can be drawn in, that is, can be made to blend with the protoplasm of the body, and can be again protruded. This fact, in connection with its conduct during fission, points to the conclusion that the collar is only the protoplasm of the anterior end of the body modified in a peculiar way, and that it may be regarded in a certain sense as a further modification of the lip-like prolongation of such an organism as Bicosœca.

The collar cannot alter its shape without at the same time changing its height. Whilst the organism is in movement it is able to contract, and the shape becomes more rounded, whilst the free edge of the collar is so much contracted that it almost closes (fig. 7 d), although its usual condition is that of a more or less funnel-shaped opening. According to Clark, the cytostome or spot where the ingestion of food takes place, is at the anterior end of the

body, near the base of the flagellum within the collar. The process of ingestion of food has not yet been fully followed out. By careful observation, however, a vacuole-like structure (fig. 7 a, α) is seen to project upon one side of the body close below the base of the collar, and beyond the contour of the body. Soon this structure disappears, and after a certain time another similar one appears upon the opposite side. It has also in some measure the appearance of wandering about close under the base of the collar; but it is not yet known whether this really happens, or whether different vacuoles rise and then vanish in opposite parts of the body. The whole matter, however, becomes simple, if it be assumed that the vacuole changes its position. The ingestion of food takes place into the middle of these vacuoles in the following way:—Particles of various kinds — Micrococci, Bacteria, &c.—are often driven by the movements of the flagellum on to the outer surface of the collar, to which they adhere; occasionally the entire outer face of the collar is seen to be covered by such adherent particles. Gradually all the particles are seen to be pushed backwards, first on to the collar, and a little later to the base of the collar, until they touch the vacuole, by which they are taken up and engulphed as food for the body. The remnants of the food are extruded close to the base of the flagellum within the collar.

The nucleus situated near the anterior end is first seen within the body, it consists in the living state of a transparent portion containing dark bodies. The nucleus becomes much more prominent after treatment with acetic acid, but there still remains the dark and somewhat granular case and the transparent exterior. The protoplasmic body is very frequently filled with a number of large non-contractile vacuoles in addition to the food vacuoles. These large vacuoles can only be distinguished from one another by their boundary walls, which are comparatively very delicate; hence the whole organism appears to be a large alveolar vacuole. The contractile vacuoles are always double, and lie at the posterior end of the body on opposite sides, not quite in the same section, since one is generally a little in advance of the other, nearly in the centre of the body's length. No third contractile vacuole was observed by Bütschli, although one has been described by Clark. The two vacuoles contract alternately; their contraction is very slow. The formation of the vacuole is peculiar, and has analogies with the same process in such ciliata as Uroleptus. The mode is as follows: — A narrow-elongated space filled

with fluid makes its appearance beneath the upper surface of the body at the spot where the last vacuole disappeared (fig. 7 c, v); this space, so far as can be determined, is formed by the flowing together of several smaller vacuoles. Shortly before the systole the space rounds itself into a vacuole.

The author has, unfortunately, failed to find the condition of division, and so has not been in a position to confirm Clark's interesting observations on this point, which are shortly as follows:—The division occurs longitudinally, and so is in conformity with the general rule amongst the Flagellata. The organisms next become globular, and the flagellum becomes shorter and shorter, till it is finally entirely withdrawn into the protoplasm. Then begins the peculiar division of the body of the organism in the neighbourhood of the flagellum, from which point it gradually proceeds backwards; finally, the collar is drawn into the division, and is gradually cut through from the base to the apex. In the meanwhile, a flagellum, which is at first small, but which gradually increases as the process of division proceeds, is budded out from the anterior end of each of the products of the fission. The posterior thread-like elongation of the body, which attaches the organism to the common stalk of the colony, also undergoes division, until finally the two products of the fission become completely separated.

The author has observed forms which were surrounded by a delicate viscid case (fig. 7 b), and also others whose bodies were covered with Bacteria (fig. 7 e).

The average size, not reckoning the collar, was 0·012 mm. The organisms have been found very frequently upon Algæ and so forth, upon the stems of *Antophysa vegetans*, and once upon colonies of *Volvox dioicus*, Cohn. They withstand a considerable degree of foulness in the water where they occur.

Salpingœca, Clark ('Ann. and Mag. Nat. Hist.,' 4th ser., vol. i, p. 199).

This genus differs from the foregoing in the fact that the animals live in transparent cups or flask-like shells; they are solitary, and not colony-forming as far as they have yet been observed; their method of reproduction is unknown.

Salpingœca gracilis, Clark? (op. cit., p. 199, pl. vi, figs. 38 and 39).

This organism (Plate vi, fig. 8) resembles Codosiga, but inhabits an elongated case, which has sometimes

the shape of a test-tube, becoming much narrower posteriorly. The author is unable to confirm Clark's statement that the hinder portion terminates in a delicate prolongation. The length of the broad tube is 0·027 mm., and it consists of a perfectly transparent firm mass, of a chitinous nature to all appearance, although no micro-chemical tests were applied to determine its constitution. In no case was the material of a viscid consistency, as stated by Clark. The organism itself occupies only a comparatively small ($\frac{1}{3}$) part of the tube, within which it is very moveable. It can stretch itself so far out that nearly the whole of the collar is extruded, or it can very rapidly retract itself to the hinder end of the tube. It is not known what causes these rapid movements of retraction, but in one case a delicate thread seemed to run from the posterior end of the body to the side wall of the tube. The co-operation of the flagellum in this action seems very doubtful. The relations of the flagellum and collar are seen in fig. 8. The flagellum is so delicate as to be scarcely visible. The ingestion of food has not been observed. The nucleus is placed anteriorly, and is made much more visible by the use of acetic acid. A contractile vacuole of considerable size is found in the hinder third of the body. The rate of contraction is slow, and the re-formation is brought about by the flowing together of several small vacuoles, which appear either shortly before or during the systole of the previous vacuole. Once it was found that after the vacuole had contracted and re-formed for some time in one place, it began instead on the opposite side of the body; this phenomenon probably gave rise to Clark's statement that there were two contractile vacuoles as in *Codosiga botrytis*.

Salpingœca amphoridium, Clark (?), (op. cit., p. 203, pl. vi, figs. 37, 37 *d*).

This species has been found only on a single occasion by the author; it agrees fairly with Clark's description. The appearance of the case is characteristically flask-like (Plate vi, fig. 9); in the form described by Clark the fixed end was rounded or somewhat pointed, whilst in this it is broadly flattened; in both cases the organism almost entirely fills the case, which thus appears to be a cast of the animal. The collar and flagellum are seen with difficulty. Numerous vacuoles are found within the body, but only one of these is contractile, whereas in Clark's *Salpingœca amphoridium* there were two large contractile vacuoles and three smaller ones. Food vacuoles are seen passing backwards

through the long neck. No nucleus was found, neither was the process of food ingestion observed.

Salpingœca Clarkii, new sp.

This organism was frequently found on the stem of *Antophysa vegetans;* it must be regarded as a peculiar species, closely allied to Clark's *Salpingœca marina*,[1] from which it differs in the form of its case, as is shown in fig. 10. The shape is comparable with that of a flower vase, and it extends behind into a delicate stem-like portion, which, as in *Salpingœca gracilis*, is a hollow and narrower portion of the case, and not a solid support, as it is in *Salpigœca marina*. The free anterior border of the case is spread out so as to be broadly funnel-shaped, and from it project the collar and flagellum. The organisms are also able to open or close the border of the calyx, and this is undoubtedly in connection with the mobility of the creatures in their cases. They are ordinarily found, like *Salpingœca marina*, in the front portion of their cases (fig. 10), but on being disturbed they go down to the bottom, so that the collar, which has become closed, only just projects above the rim of the calyx. In this condition it is very difficult to distinguish the collar. The flagellum is readily visible, and is generally quite motionless and slightly extended. The ingestion of food has not been followed, although there are usually a number of particles, which are undoubtedly food particles, lying in the body. The nucleus is easily seen, and lies, as in other forms, anteriorly; its structure is the same as in Codosiga and *Salpingœca gracilis*. The contractile vacuoles are present, situated on opposite sides of the body, as in Codosiga, or close to each other, as in fig. 10. The height of the calyx is 0·019 mm.

As an appendix to the genus Salpingœca a small organism is here mentioned, which was pretty frequently found upon the stem of *Antophysa vegetans*, and of whose exact position the author is not quite certain, on account of the great difficulty in studying a new organism of such minuteness. These small Flagellate organisms inhabit a case fixed upon the stems of Antophysa, as seen in fig. 11, a c, which shows varying forms. The walls, which are of considerable thickness, are of a deep brown colour, and have an irregular and rough contour. The height of the case is about 0·008 mm. The protoplasmic body generally fills the case, and may either extend beyond it to a greater or less extent, or not at all, At the anterior extremity, which extends beyond the case

is seen the flagellum, which is sometimes vibrating (fig. 11, a). On either side of the flagellum is seen, though with great difficulty, a faint line, which resembles the optical section of the collar in Salpingæca. Frequently neither the flagellum nor collar is visible (fig. 11, c), or the latter appears to be shrivelled, in which case the organism is remarkably like a rhizopod. A nucleus lies within the more or less granular protoplasm, and near it are (fig. 11, a), one, and in some cases three contractile vacuoles (*v*), lying at the hinder end of the body (fig. 11, *c*).

Bicosœca, Clark ('Ann. and Mag. Nat. Hist.,' 4th ser., vol. i, p. 139).

Stylobryon, Fromentel ('Études sur les Microzoaires).'

Small organisms with a single long flagellum at the anterior end, together with a large lip- or beak-like prominence for the ingestion of food. A contractile vacuole is present, and a nucleus doubtfully so. Each individual, like Dinobryon, inhabits a calyx-like case, into which it can retract itself with the assistance of a very elastic thread which springs from the posterior end of the body. Occasionally, as in Dinobryon, colony-building forms are observed. These organisms are found both in salt and fresh water.

Bicosœca lacustris, Clark (?), (op. cit., p. 188, pl. v, figs. 33, 33 *c*).

This species is very frequent in ponds, where it attaches itself to Algæ and other water plants, and often to the main stem of Antophysa. Solitary individuals are generally observed, whose calyx is attached to a delicate stem. In the forms observed by Clark this stem reached at the most only half the height of the calyx, but in those seen by Bütschli the stem far exceeded the calyx in length (fig. 12, a). Occasionally colony-building forms have been noticed (fig. 12, a b.) The young calyces are produced from the mouths of the older forms, just as they are in Dinobryon. A dark supporting line has several times been seen to extend from the posterior end of such a young specimen to the older one (fig. 12, b), and consequently it must be asserted that the young calices are provided with stalks, which extend from the inner wall of the older ones.

The shapes of the calyx are seen in the figures. The openings are either rapidly enlarged as in fig. 12, b, or as rapidly narrowed (fig. 12, c and d), and it can sometimes be clearly seen that the opening is nearly closed, when the

animal withdraws itself into its calyx, although this is by no means always the case (fig. 12, b). Clark was probably right when he attributed this power of closing the shell to young forms. Sometimes the calyx is not circular, but is triangular. Of this, however, the author is not quite certain.

The height of the calyx is, on an average, 0·014 mm. The organism is attached to the base of it by means of a thread springing from the hinder end of the body; it is this thread which Clark rightly compares with the hinder flagellum of many heterotrich Flagellata, as, for instance, many forms of Cercomonas. The contractile vacuole is a little distance rom the point of origin of this thread of attachment. The flagellum, of considerable length, springs from the anterior end and stands out straight from the body when it is in its usual state of rest (fig. 12, c). The extreme end alone vibrates or bends at this time, throwing the minute particles of food with considerable force against the beak-like prominence. When, however, the organism is retracted into its case the flagellum is rolled up (fig. 12, b) so that it is protected by the case.

The lip- or beak-like prominence for the reception of food is very noticeable, and appears to resemble most nearly the one found in Antophysa. It is seen, by observing it in different positions, to be strictly a leaf-like broadened prolongation (fig. 12, c and d). A vacuole formed before the ingestion of food has never been observed, but one is produced as soon as a small particle of food has been thrown between this prominence and the base of the flagellum. The vacuole so formed takes in the food and distributes it in the body. Clark placed the mouth at this spot, although, there is no doubt, that no such orifice exists preformed for the reception of food, but only that a particular spot on the surface of the body is set aside for this purpose. Clark has observed that the food remains are extruded a little above the spot at which the food is ingested, but the author has not yet followed out the act of defæcation.

Nothing is noticeable in the body proper of the organism. Clark, however, has observed in the two species of this genus which he examined, a furrow extending along the whole length of the body, beginning at the base of the flagellum, and traceable to the point of origin of the posterior thread of attachment. He believes that this groove is distinguishable by a peculiar contractility. The body itself is possessed of a certain contractility, as it has been seen to become spherical without the aid of the posterior thread. The nucleus has

not been observed by the author, although he does not doubt but that it is present.

The process of reproduction has not been followed, but it almost certainly increases by fission, like its fellows. In the formation of a colony one of the young buds, as in the case of Dinobryon, settles upon the rim of the old calyx, and builds there a new case for itself; and in this way from a single one arise the compound trees of a great number of individuals. Clark has found a second variety of this species, *Bicosœca gracilis;* it is a marine form.

The *Stylobryon insignis* of Fromentel[1] forms definitely a third kind, which differs chiefly from *Bicosœca lacustris* in the fact that each calyx of the colony possesses its own very long stem; this form stands somewhat in the same relation to *Bicosœca lacustris* as *Dinobryon petiolatum* Duj. to the ordinary *Dinobryon sertularia.*

Dinobryon, Ehrbg ('Die Infusionsthiere als vollkommene organismen,' Leipzig, 1838, p. 124).

Dinobryon setularia, Ehrenberg (op. cit., p. 124, pl. vii, fig. 8).

Dinobryon, Dujardin ('Histoire Nat. des infusoires,' Paris, 1841, p. 321, pl. i, fig. 2).

Dinobryon, Perty ('Zur Kenntniss kleinster Lebensformen nach Bau, Function, Systematik,' &c., p. 178).

Dinobryon, Claparède and Lachmann ('Études sur les Infusoires,' p. 65, pl. xii, fig. 66).

Dinobryon, Fromentel E. de ('Études sur les Microzoaires,' Paris, p. 336, pl. xxvi, fig. 1).

Of this beautiful form Bütschli states that he has found only free swimming colonies (Plate vi, fig. 13). The vase-like case of the individual organisms calls to mind the very similar cases in Bicosœca and Salpingœca, whilst the grouping of the individuals to form a colony is just like the arrangement in *Bicosœca lacustris.* The young calyces also grow from the inner side of the free edges of the old forms, generally single but occasionally double. The organisms are of a yellowish-brown or green colour, the colours proceeding, as in many coloured Flagellata, from two pigment discs, which are placed side by side on the colourless protoplasm of the body (fig. 13 a and 13 b). Of these discs one is generally the longer, and extends further forward than the other. Ehrenberg noticed that the small inhabitants of the cases were very contractile; from the anterior end springs a rather

[1] Op. cit., p. 336, pl. ix, figs. 12—14; pl. xxvi, fig. 8.

long flagellum of even thickness throughout; it generally moves along its whole length with a serpentine, less frequently with a rolling, motion. The author has noticed a small accessory flagellum close to the flagellum known to Ehrenberg. The accessory flagellum is generally at rest in an extended condition. Bütschli also believes that he has seen a delicate thread arising from the posterior end of the body, and attaching it to the base of the case. The eyespot lies close to the base of the flagellum, whilst the two contractile vacuoles are close to each other at the hinder portion of the anterior third of the body; the contraction of these vacuoles is quick and sudden. Föcke[1] was the first to recognise a single contractile vacuole in these organisms, and after him Claparède described and figured them. No nucleus was observed by Bütschli, as the little free-swimming colonies are difficult to treat with reagents. Occasionally a group of small granules of high refractive index were observed in the hinder third of the body; it cannot be decided whether the minute organisms take solid food. Fromentel has lately described a dark cytostome at the base of the flagellum; he appears to have mistaken the eyespot in this way.

As regards the formation of a colony, the following points are noticed by Bütschli:—The colony is doubtless formed by fission of the organisms in their cases, but the actual fission has not yet been followed out. Calices have, however, been seen, which, in addition to an individual situated at the bottom, have a second caseless form placed at the mouth of the calyx (fig. 13 b). It appears to be proved that these two individuals have proceeded from the fission of the previous inhabitant of the calyx, since each contains only a single pigmented disc, whilst the anterior one alone possesses an eyespot. Carter has observed a somewhat similar phenomena in the fission of his *Euglena agilis* in its encysted state, for the hinder product of division is in the same way devoid of an eyespot. The anterior organism, in a more advanced stage, is attached to the mouth of the calyx by its posterior pointed extremity, and then a small calyx forms round its hinder half.

A large cyst (fig. 13, a, *c*) has been seen at the mouth of an empty calyx; it consisted most exteriorly of a coarse sheath containing a smaller excentric sheath; this in turn was filled with a protoplasmic contents and the two characteristic pigment discs. No eyespot was visible, but the

[1] 'Physiologische Studien,' Hft. 2.

author believes that these cysts bear some relation to *Dinobryon sertularia*. The formation of the two sheaths calls to mind the condition in *Nucleoria simplex*, which was first observed by Cienkowski.

Trepomonas, Dujardin ('Histoire nat. des Infusoires,' Paris, 1841, p. 294).

Trepomonas agilis, Dujardin (op. cit., p. 294, pl. iii, fig. 14).

Trepomonas agilis, Perty ('Zur kenntniss kleinster Lebensformen nach Bau, Function, Systematik,' &c., p. 171, pl. xiv, fig. 15).

Trepomonas agilis, Fromentel ('Études sur les Microzoaires,' Paris, p. 334, pl. xxvii, fig. 16).

Grymæa vaccillans, Fresenius ("Beiträge sur Kenntniss kleinster organismen," 'Abhl. der Senkenberg. Geschellsch. zu Frankfurt-a-M.,' Bd. ii, pl. x, figs. 48, 49).

This is one of the most interesting of the Flagellate forms; it is tolerably common in rather dirty water, and is sometimes found in immense numbers in infusions. The organisms are difficult to observe properly, on account of their almost constant and peculiar screw-like movement. The organism is oval and somewhat flattened (Pl. VI, fig. 14, a, b, c), the hinder end is generally broader in a noticeable degree than the anterior. The long sides are drawn out and broadened into delicate wings, which are bent outwards laterally, in contrary directions, towards the broad sides, in such a way that the transverse section of the body presents the form of an S. These reflexed expansions are small and feeble at the anterior end of the body, increasing gradually as they pass backwards, till they present a considerable surface. The flagella are always, when the organism is observed laterally, directed obliquely away from the body (fig. 14, *b*). In a surface view from above (fig. 14, *a*) they are seen to be bent in such a way as to correspond with the screw-like expansions, and are uniformly thick filaments. As a result of this arrangement of the flagella the little organisms move through the water with rapid undulations, the screw-like end backwards, and the flagella in front. The internal arrangement of these little living screws is just as interesting as the external formation. Trepomonas is undoubtedly an animal Flagellate, which ingests solid nutriments, although the precise spot at which it is taken in has not been observed. The numerous food particles, such as Bacteria, enclosed in the very clear and transparent protoplasm, leaves no doubt as to its mode of nutrition. The author has been unable to

discover the mouth lying terminally, according to Diesing's[1] statement. Very interesting are the active movements of the protoplasm to be observed in the organism at rest. These cir cular streamings, which are recognised by the rapid displacements of the very numerous vacuoles and the contained particles, occur regularly, but with a motion which is sometimes slower, and sometimes more rapid, whilst often the direction of the stream is entirely changed. The relation of the contractile vacuole is also interesting (fig. 14, c). Here and there in the protoplasm vacuoles are seen to circulate, such vacuoles, remarkable for their size, being pushed towards the screw-like posterior end; after some time they contract. This condition of the vacuole calls to mind a similar one in various Amœbæ, *e.g. Amœba guttula*, Duj., *limax*, Auerb., and others, in which the vacuole, after being formed in the protoplasm of the body, has been seen to contract at the posterior extremity of the moving animal. The nucleus is best seen either in a dying organism or in one lately dead, as a rounded, pale body, of considerable size, in which, sometimes but not always, a small clear area is visible. Its position is constant at the anterior extremity of the body (fig. 14, *c*.) and frequently, instead of one such nucleus, two are found lying close together. Reproduction is by transverse fission, according to Perty, but the author is doubtful on this point.

Hexamitus, Dujardin ('Histoire nat. des Infusoires,' Paris, 1841, p. 296, pl. iii, fig. 16).

Hexamitus inflatus, Dujardin (op. cit., p. 296).

Dujardin has described three forms of this characteristic genus, which he has called Hexamita, from the sextuple arrangement of the flagella. Of these forms two, *Hexamita nodulosa* and *inflata*, are found in foul marsh water, whilst the third, *Hexamita intestinalis*, is parasitic in the intestine and body cavity of the frog and newt. Bütschli is inclined to believe that these are only two varieties, differing somewhat, of a single species, which are most nearly related to the form *inflata*, and he has consequently chosen this name for both the forms. The Flagellata in question were only once found, and that in foul marsh water; they are not very common. Their appearance is somewhat variable; they occurred at first in the extended form (fig. 15, a), but at a later period, and much oftener, they were found as short, rounded organisms (fig. 15, b). This shape appears to change very easily, since such a form as fig. 15, b, lying at rest, has

[1] "Revision der Prothelminthen," 'Sitzungsber. d. k. Acad. zu Wien,' 1865, Bd. lii, p. 323.

been seen to gradually assume an active condition, and then to take on the more elongated form. Sometimes the organisms appear to have such power of change that their outline becomes irregular, and they even exhibit amœboid movements. The protoplasm of the Hexamiti is very clear and transparent, as in *Trepomonas agilis* and *Pyramimonas descissa*. In the first form there are some interesting agreements as regards the relations of the contractile vacuoles. There is much difficulty in determining the exact number of the long flagella, but Bütschli believes that he has been able, from observations on living specimens as well as on those killed by treatment with chromic acid and solution of iodine, to fix the number at eight. Of these eight flagella two spring from the hinder corner, which is either blunt or slightly indented; as Dujardin has observed, these two flagella are drawn along by the general movement, without themselves moving to any great extent. The organisms also attach themselves for a time by this posterior pair of flagella, and rotate rapidly on their axes, as if anchored. In addition to these, three flagella, the active agents in causing motion, arise on each side of the body; they are of very considerable length. The protoplasm of the body is in part quite free from granules, and is, therefore, transparent; in part, however, there are considerable numbers of granules of varying size, and of a dark nature; many Hexamiti also contain a number of long, very dark and shining bodies (fig. 15, *b*), which sometimes entirely fill up the interior of the organism, occasionally similar bodies, of a dark brown colour, are visible. No investigations into the chemical nature of these bodies has been made, but as they are frequently found swimming freely in the water, which is inhabited by the Hexamiti, there is no doubt that the latter take them in as solid food, although the exact mode is still unknown. A single nucleus has often been clearly observed about the centre of the body (fig. 15 a, *n*); it is of the same nature as in *Trepomonas agilis*. A contractile vacuole is situated at one side and another at the posterior extremity (fig. 15, *a*, *b*). After the contraction the following curious phenomenon occurs during the re-formation. An elongated clear space, filled with fluid, makes its appearance near the spot where the previous vacuole disappeared; this space rapidly becomes round, and is then slowly pushed forwards through the body, it soon turns back until it reaches the spot at which the previous vacuole contracted; the systole then occurs. Sometimes the new vacuole is produced before the systole of the previous one, but after this has taken place the new one is pushed to the hinder end, where it contracts.

This phenomenon of the vacuole presents considerable likeness with the appearances observed in Trepomonas. The length of the Hexamiti was about 0·01 to 0·02 mm. Fission alone of the processes of reproduction has been observed, and that not in detail.

Pyramimonas, Schmarda ('Neue Formen von Infusioren: Denkschrift der k. Acad. d. W. zu Wien. M. Naturwissensch. Classe,' Bd. i, 1850; 'Abhandl. von Nichtmitgliedern,' p. 9, pl. iii, fig. 1).

Tetramitus, Perty ('Zur Kenntniss kleinster Lebensformen,' p. 170).

Pyramimonas descissa, Perty (op. cit., p. 170, pl. xiv, fig. 3).

This is, again, an exceedingly interesting species, of which two distinct forms appear to be known, the one described here, the other, *Tetramitus rostratus,* of Perty,[1] which has been figured by Fresenius,[2] without further description.

Pyramimonas descissa is a small organism which Bütschli has only once found in any quantity; it occurred in foul pond water. The appearance of the organism is elongated, and is rightly described by Perty as being cone-shaped (Pl. VI, fig. 16, a), since the hinder end is the more pointed, although this is not regular, as this end is sometimes quite round, as fig. 16, b. The anterior extremity is exceedingly typical, for it is sharply oblique, so much so, indeed, that the oblique surface is slightly inclined towards the axis of the organism so as to embrace the entire anterior extremity of the body. The oblique surface is concave. Anteriorly are four flagella, of which the posterior is the shortest, whilst the most anterior is the longest. By means of these flagella the organism rotates rapidly and regularly, and consequently its examination is attended with difficulty. The very clear protoplasm of the body contains numerous dark granules, which give the impression of being food particles, since they are in many cases enclosed in large vacuoles. That such is actually the case is proved by the fact of such particles having been seen to be thrust out of the body. The simple contractile vacuole lies at the hinder end of the body (fig. 16, a, and b, *v*); it contracts rapidly and suddenly. Two small and fresh vacuoles appear before the systole of the previous vacuole begins; after this

[1] Op. cit., pl. xiv, fig. 4.
[2] Pl. x, fig. 34, 35.

has disappeared these two coalesce and increase. The newly-formed vacuoles are not found exactly in the same position, but they appear to occur alternately on each side. No nucleus has yet been seen with any certainty. Reproduction occurs, according to Perty, by longitudinal fission.

Chilomonas, Ehrb. ('Die Infusionsthiere als vollkommene organismen,' Leipzig, 1838, p. 130).

Chilomonas, Dujardin ('Hist. nat. des Infusoires,' Paris, 1841, p. 295).

Cryptomonas, Perty (p. 165).

" Ehrb. (p. 2).

Zygoselmis, Fromentel (p. 2).

Moderately elongated Flagellata, whose anterior end is divided into two lips, between which is a distinct cytostome (cell mouth), bounded by dark and closely-applied walls which run far into the body. At the anterior end are two fair-sized flagella. A contractile vacuole is present in the upper lip, whilst a large nucleus is situated posteriorly. Reproduction takes place by longitudinal fission.

Chilomonas paramecium, Ehrb. (op. cit., p. 30, pl. ii, fig. 6).

(?) *Cryptomonas curvata*, Ehrb. (p. 40, pl. ii, fig. 16).

(?) " *cylindrica*, Ehrb. (p. 42, pl. ii, fig. 19).

" *polymorpha*, Perty (p. 162, pl. xi, fig. A—H.)

Chilomonas granulosa, Dujardin ('Histoire nat. des Infusoires,' Paris, 1841, p. 295, pl. iii, fig. 15).

Chilomonas paramecium, Ehrb. (Schneider, A., "Beiträge zur Naturgesch. der Infusiorien," p. 199, p. ix, fig. 25; 'Arch. f. Anat. und Physiol.,' 1854).

(?) *Chilomonas obliqua* (Duj.), Fromentel (p. 331, pl. xxiii, fig. 35).

Zygoselmis nebulosa (Duj.), Fromentel (p. 320, pl. xxiii, fig. 25).

These organisms are amongst the most frequently occurring Flagellata, particularly in somewhat foul ponds and in infusions. In infusions, however, only a colourless kind are found, generally as a dark variety enclosing a great number of large and dark granules—the true *Chilomonas paramecium* of Ehrenberg, or the *Chilomonas granulosus* of Dujardin. The brown or green variety, to which both species of Ehrenberg's Cryptomonas belong, are only found in ponds.

The shape of the organism is very variable (Plate

VI, fig. 17, a, c), as the end which is devoid of flagella is sometimes pointed, sometimes rounded, and sometimes is bent into a sharp hook-shape, and again, may be without any such bend. The colourless examples from infusions are generally small, about 0·022 mm., whilst the brown forms from the ponds are, for the most part, proportionately very large, attaining a length of 0·049 mm.; others, however, only attain a length of 0·015 mm., and consequently, are very small. There is so little variety amongst them, that the author believes, with Perty, that they are all of one species. The anterior end is considerably wider than the posterior, and the lip is well marked, although it is so far back that the cleft shows but little at the anterior end. The two flagella in front are of equal length and strength. The strength of the flagella is considerable and does not lessen towards the end. The deportment of these flagella during the state of rest is very peculiar, for the organisms frequently tuck them in, rest for a considerable time, and then make them suddenly revolve with great rapidity. The two flagella frequently assume during the resting state the positions shown in fig, 17, c, but they are also frequently seen in very cramped positions. The point of origin of the two flagella is not accurately determined, but they appear to arise at some distance from each other, probably one from the upper and the other from the lower lip, as is figured in fig. 17, c. The cytostome (mouth opening) is situated between the two lips. It leads into a short tube which is quite transparent, and which is bounded by thin walls; this leads into the gullet provided with thick and dark walls (fig. 17, a, and c, œ). This cavity, as seen from the surface, appears to be striped longitudinally as well as transversely, so that a knotted appearance is seen at the points where the two systems cross each other; the walls, therefore, in optical section, appear to be knotted (fig. 17, a). The substance of which these walls are composed seems to be thickened protoplasm, because they do not remain after the death of the animal, but are destroyed. The ingestion of food has not been satisfactorily followed out, but they appear to take in food in the same way as do the other Flagellata.

The contractile vacuole is situated in the upper lip, where it is easily visible; the contractions occurring but slowly, it requires attention to observe them; this, however, Stein has accomplished.[1]

In the coloured varieties, the pigment is by no means

[1] Fr. Stein, 'Die infusionsthiere auf ihre Entwickelungsgeschichte untersucht,' Leipzig, 1854, i, p. 91.

evenly distributed throughout the body, but, as in other coloured Flagellata, there are found two pigment discs of moderate thickness (fig. 17, *a*). These discs lie close below the surface of the body, and are so closely approximated along the shorter and longer sides of the body that only a small light space separates them (fig. 17, *b*.)

The vesicular nucleus, with its large inner body, lies at the anterior boundary of the posterior third of the body; in dead specimens a thickened wall may be seen surrounding the vesicle of the nucleus. The granules, which lie in a double row in the interior of the body, consist mainly of starch, as has been already shown by Schneider, although many do not contain this substance. Iodine causes a blue colouration in the starch granules, which disappears on the addition of concentrated sulphuric acid, although there still remains a considerable number of yellowish or reddish-brown corpuscles. Sometimes in old specimens, starch appears to be absent, and only a few small granules of high refractive index are present. In such cases the protoplasm of the body is crowded with vacuoles, so that it appears to be hollow and alveolar, without resulting injury to the organism. One very remarkable observation has been made by Bütschli. After treatment with acetic acid of 1 per cent. the appearance seen in fig. 17 g was obtained. A number of fine rays shot out from the dead animal in all directions, so that the appearance was like that of a Paramœcium, in which all the trichocysts have been extruded. Amongst the rays were here and there entangled a few granular masses. The author puts forward, as an explanation of this phenomenon, that the organisms have an arrangement which is similar to the trichocysts of the Ciliata, qualifying this, however, by the statement that no such formation has yet been observed in the living organism. The animals are very sensitive, and have been observed to die rapidly under the cover glass; their bodies becoming rounder and rounder, and finally collapsing. Reproduction by longitudinal fission has as yet been alone observed, as seen in (fig. 17, d and f). In the single case observed by the author, the flagella of the daughter individuals were present before the pinching off occurred, without their origin being traced. The constriction occurs tolerably evenly along the whole surface of the body (fig. 17, d), but probably somewhat earlier at the posterior extremity, since the products of division remain joined for the longest period at the centre of the body. In the pinched-off portion of the body, which is tolerably transparent (fig. 17, d), are a number of dark

lines running transversely; these appear as if the dark granules of Chilomonas had been elongated, although this cannot be proved. These transverse stripes are seen more distinctly in fig. 17, e. The pinching-in proceeds very rapidly in a forward direction, so that in a few minutes the two organisms are only attached to each other by a very delicate thread, situated somewhat above the centre of the body (fig. 17, f). This thread then breaks, and the resulting organisms are free. The relations of the nucleus and contractile vacuole at the time of fission were obscured by the movement of the organism and the opaqueness of the protoplasm.

Astasia, Ehrenberg ('Poggendorf's Annalen,' 1830, p. 508).

Trachelius, Ehrenberg ('Die Infusionsthiere als vollkommene organismen,' Leipzig, 1838, p. 320).

Peranema, Dujardin ('Hist. Nat. des Infusoires,' 1841, p. 352).

Astasia, Dujardin (op. cit., p. 356).

Pyronema (Duj.), Diesing ('Revision der Prothelminthen Sitzungsbericht. d. k. Acad. zu Wien,' 1865, Bd. iii, p. 327).

There is some doubt as to the classificatory position of these organisms, of which there appear to be three species. Peranema and Astasia differ from each other in that the former has a rounded extremity, whilst the latter has a tail-like and pointed posterior end, but this difference is of slight importance, since the forms are exceedingly variable. Both Peranema and Astasia have the mouth situated terminally, whilst in Pyronema it is ventral.

Astasia trichophora, Ehrenberg.

(?) *Trachelius trichophorus*, Ehrenberg ('Abhandl. d. Ak. d. W. zu Berlin,' 1830, pp. 54, 65, 70; and 'Die infusionsthiere als vollkommene organismen,' Leipzig, 1838, pl. xxxiii, fig. 11).

Peranema protracta, Dujardin ('Hist. Nat. des Infusoires,' Paris, 1841, p. 354).

Peranema protractum, (Duj.), Perty ('Zur kenntniss kleinster Lebensformen nach Bau, &c.,' p. 108).

(?) *Astasia limpida*, Dujardin (op. cit., p. 357, pl. v, fig. 12).

Astasia limpida (Duj.), Carter ("Notes on the Freshwater Infusoria of the Island of Bombay," 'Ann. and Mag. of Nat. Hist.,' 2nd ser., vol. xviii, p. 115, pl. vi, figs. 45—48).

Astasia trichophora, Claparède ('Études sur les Infusoires,' pp. 41—346).

Astasia trichophora, Clark ('Ann. and Mag. Nat. Hist.,' 4th ser., vol. i, p. 250, pl. vi, fig. 45).

These organisms appear undoubtedly to possess a mouth; Pl. vi, fig. 18, *a*, represents a specimen which measures across the centre 0·05 mm. The form is very variable, owing to the capability of energetic contraction possessed by the body; apparently due to the partial contraction of the outer layer. These layers are usually arranged in rings round the body, so that in individual zones there is at one line an increase, and at another a decrease in size, and in consequence the whole either elongates or contracts. The greatest amount of contraction causes the body to assume an almost spherical shape. In large specimens the author has observed a fine and delicate spiral striping of the outer layer of the body surface, resembling the condition seen in *Euglena viridis*. The anterior end of the body which carries the flagellum, is generally somewhat narrowed, and is sharply truncate; the animal moves slowly, with a sliding and tolerably constant motion. The flagellum is considerably larger than the body when extended to the full; it is carried quite straight and fixed, and the extremity alone performs vibrating movements. Specimens with no flagella are occasionally met with; in such cases movement is effected as in Euglenæ with no flagella, by the contractility of the body; such organisms are probably in the act of becoming encysted. The posterior end is generally rounded and is never pointed, as described by Clark. The author is also unable to verify Clark's description of an eyespot.

The mouth apparatus, of which it is not easy to give an account, is situated at a short distance behind the base of the flagellum. A thick dark band is seen upon one of the flat surfaces of the body, not far from the base of the flagellum (fig. 18, *a*), which can be traced backwards for a longer or shorter space, becoming gradually narrower, till it ultimately disappears. This band has been seen to consist of two lines, lying so close to each other as to appear as a nearly closed tube when seen in optical section. At the front end of the band a transparent circle is often seen, together with one or two delicate streaks which run off to the base of the flagellum (fig. 18, *a*). The posterior double stripe will, upon this hypothesis, be the walls of what is usually a closed œsophagus, which arises from a chink-like cytostome situated between the anterior end of this band and the base of the flagellum. The mode in which

food is ingested gives strength to this theory, for *Astasia trichophora* has been seen to swallow large spherical bodies (fig. 18, *b*) of unknown nature. The portion of the body close behind the base of the flagellum, where the slit-like cytostome is situated becomes funnel-shaped, and surrounds the food to be ingested. In this funnel is seen a transparent tube of considerable size, whose walls appear in optical section as delicate bands; this tube leads backwards, and is the œsophagus distended for the reception of food; along it the food materials pass, without any assistance from the flagellum, into the interior of the body. Stein has observed the expulsion of food remains from the posterior end of the body. The contractile vacuole is at the anterior end close to the œsophagus. The contraction is rapid and very sudden, according to Clark. After the contraction several small vacuoles appear, which coalesce to form the new vacuole. In one specimen an elongated space filled with fluid made its appearance, after the contraction of the vacuole, near one or two small vacuoles in the position of the old one; the small vacuoles which ultimately coalesced appeared to fuse with this space. The large vesicular nucleus, with dark inner bodies, lies near or somewhat behind the middle of the organism. Within the protoplasm of the body is seen the food, which is not enclosed in vacuoles. Peculiar reddish-brown bodies are also present, as also brownish or brownish-green granules of secretion. These granules are either scattered throughout the protoplasm, or they are collected chiefly in the posterior portion of the body. They closely resemble in their very characteristic appearance the secreted granules met with in the Ciliata and in Amœbæ, and are remarkable for their peculiar brownish-green, olive-like pigment, and in Amœbæ for their clearly crystalline form. The form of the crystals, as well as their reactions, show that oxalate of lime is present.

Anisonema, Dujardin ('Hist. Nat. des Infusoires,' p. 344).

Bodo, Ehrenberg ('Die infusionsthiere als vollkommene organismen,' Leipzig, 1868, p. 34).

Heteromita, Dujardin (op. cit., p. 297).

(?) *Heteronema*, Dujardin (op. cit., p. 370).

These organisms possess two flagella, situated at the anterior extremity, which are sharply differentiated from each other by their different conduct in motion. The shorter flagellum, which springs from the anterior wall in advance of the other, is the one by the vibrations of which alone the

forward movement is effected. The larger flagellum rising somewhat further behind is directed backwards by the movement, and so it often simply trails till it attaches itself, and then, by its rapid bending movements, it throws the body backwards and forwards, but chiefly backwards, upon the same spot. It is this flagellum to which Clark, in contrast to the first one, has applied the term "gubernaculum."

An integument is present, which has been investigated, with a view to separating the three genera included here under one name. Forms of unvarying shape, the surface of which did not appear to be of a sticky nature, so that foreign bodies adhered to it, were considered as being provided with a firmly resisting integument, or a coat of mail, and were placed in the genus Anisonema; whilst on the other hand the genus Heretomita was recognised by the absence of such an integument. Mobile forms, such as Euglena and Astasia, are distinguished by the possession of a contractile integument, and this character serves also to differentiate the genus *Heteronema*.

As numerous Euglena-like organisms are known to possess a very resisting and cuticle-like covering, so it is possible that this character sharply differentiates in some degree the genus Heretomita. On this account the author has had some hesitation in associating Heteromita of Dujardin with the organisms now described.

Anisonema acinus, Dujardin ('Hist. Nat. des Infusoires,' Paris, 1841, p. 345, pl. iv, fig. 27).

(?) *Heretomita orata*, Dujardin (op. cit., p. 298).

Anisonema concavum, Clark ('Ann. and Mag. Nat. Hist.,' 4th ser., vol. i, p. 254, pl. vii, figs. 65—69).

Heteromita crassa, Fromentel ('Études sur les Microzoaires,' Paris, p. 335, pl. xxiii, fig. 16).

Diplomita insignis, Fromentel (op. cit., p. 335, pl. xxxiii, fig. 37).

This is a somewhat flattened organism; the ventral surface, upon which it generally advances, appears hollowed so as to be slightly concave, whilst the dorsal surface is correspondingly convex. The outline of the broad sides is nearly oval, and usually the hinder part is somewhat broader than the anterior, which is somewhat pointed, although—as a comparison of fig. 19 a with 19 c will show—there is no rule in regard to this. The small flagellum causing movement arises from the most anterior point of the organism. The concavity of the ventral surface is not quite in the centre; but extends somewhat lower on the right side by the

wall of which it is limited. The arched form extends round to the anterior wall, and then disappears at the point of insertion of the posterior flagellum. This flagellum arises somewhat to the left of the middle line, like the cytostome (cell mouth), and runs along the inner side of the arch in a curve to the anterior extremity, round the cytostome, and backwards along the right side of the ventral surface.

Somewhat behind the point of insertion of the posterior flagellum, and on the left side, is the contractile vacuole (fig. 19 a, *c*). The mouth apparatus is seen on the inside of the portion bounded by the anterior curved part of the posterior flagellum as a tube-like structure, which does not extend very far back. The nucleus is seen without difficulty, as an oval tolerably large body, at the posterior end of the organism on the right wall of the body. It differs somewhat from the nuclei of the Flagellata which have yet been described, approaching more nearly to the nucleus of the Ciliata, as it exhibits granular bodies as dark as the surrounding protoplasm. In the protoplasm itself are seen a greater or less number of secreted granules, as in Astasia, which are chiefly aggregated at the posterior end of the body. Nothing has been observed by the author in relation to the reproduction, although multiplication undoubtedly proceeds by longitudinal fission.

Anisonema sulcatum, Dujardin ('Hist. Nat. des Infusoires,' Paris, 1841, p. 345, pl. iv, fig. 28).

Bodo-(?) grandis, Ehrenberg.

Anisonema sulcatum, Perty ('Zur kenntniss kleinster Lebensformen,' p. 164).

These organisms are tolerably common, measuring 0·02 mm., and being of a distinctly oval form (fig. 20 *a*) ; they are not quite so much flattened as is *Anisonema acinus*. The peculiar flattened ventral surface, which was described in the previous form, is here wanting. The posterior flagellum runs directly backwards without describing the peculiar curve at the anterior end. The anterior small flagellum which causes motion arises usually from a distinct, but sometimes from a somewhat obscure, notch at the anterior end, somewhat to the left of the middle line. The long posterior flagellum is inserted a short distance behind upon the ventral surface, at exactly the same point as in the preceding species. This species attains to nothing like the size of the preceding. The mouth apparatus, commencing at the most anterior point of the body, runs backwards exactly in the middle line; it is distinctly tube-like, becoming gradually smaller towards the

posterior end until it reaches the hinder third of the body. Bütschli's hypothesis is that this apparatus is nothing but an œsophagus, which, beginning at the anterior lip-like end of the body, sinks into the body. The ingestion of food has not been watched. Both the dorsal and ventral surfaces are more or less distinctly ribbed longitudinally, but this is sometimes scarcely perceptible.

The contractile vacuole is in exactly the same position at the base of the flagellum, as in the preceding species. The nucleus lies on the same side of the body, somewhat towards the centre; it possesses the structure that is usual amongst Flagellata, viz. the vesicular, with a large dark inner body. A considerable number of secretion granules is found in the body protoplasm, in addition to the food elements. A considerable number of observations have been made on these organisms in relation to the process of fission. Individuals which are preparing to undergo this process show the longitudinal banding much better and more clearly than is the case in ordinary specimens, in which there is often no trace of this ribbed appearance, although, as already remarked, it appears very clearly during the fission (fig. 20 b).

The earliest condition of division which the author has observed shows the flagella for both the young forms in full perfection, close to each other, at the anterior end of the somewhat compressed organism (fig. 20 b). The method of the formation of these flagella was not followed out, but, so far as is known, it does not appear to occur in the way described by Dallinger and Drysdale[1] for a very much smaller Flagellate, 0·0085 mm., of Anisonema-like form. The pair of contractile vacuoles for the two offspring are present before the constriction of the body takes place, and this remark should apply also to the mouth apparatus, but on this point observations are wanting. The actual longitudinal division of the body of Anisonema occurs in a one-sided way, for the constriction between the flagella begins at the anterior boundary, and gradually pinches through the body backwards, without any constriction occurring from behind (fig. 20 c—f). Finally, the two young offspring hang together by their posterior ends only by a delicate thread, which is ultimately broken through. After treatment of one of these dividing organisms with dilute acetic acid the condition of the nucleus is rendered visible.

[1] "Further Researches on the Life-history of the Monads," 'Month Micros. Journ.,' 1873, Vol. X, p. 245.

Shortly before or at the instant of appearance of the mark of fission the nucleus appears band-like and elongated across the body of the organism (fig. 20 c). There also appears to be a longitudinally-striped differentiation of the inner substance of the nucleus, and a swelling of this stripe into knot-like thickenings is to be clearly seen at one of their ends. After the fission had made some progress the nucleus thinned in the middle, the ends became swollen, and in each a distinct inner body made its appearance, connected by a delicate thread with the one on the other side (fig. 20 f). In a still more advanced condition the two nuclei, which had become quite rounded, were only united by a delicate thread of considerable length.

Lophomonas, Stein ('Sitzunbericht. der. königl. böhm. Gesellsch. d. Wissensch. Jahrg.,' 1860, pp. 49, 50).

Lophomonas blattarum, Stein (loc. cit.).

These highly interesting parasitic Flagellate forms were found by Stein in the rectum of *Blatta orientalis*. The author is able to confirm Stein's observations in every respect, so far as the few specimens seen by him will allow. The shape of *Lophomonas blattarum* is a roundish ovoid (Plate vi, fig. 21 b), only the smallest individuals possessing the more spherical form (fig. 21 a) described as being most common by Stein. The author has investigated these organisms in a dilute solution of albumen, and has by this means avoided the alterative influence of water, whilst he has been able to preverve them uninjured for more than twenty-four hours.

The somewhat tapering anterior extremity is sharply truncated, and it is from this point, which is sometimes very distinct, and at other times very indistinct, that the tuft of flagella which is so characteristic of the species arises. This tuft consists of a great number of flagella ranged close to each other which are in part twisted together into a tuft—this is true chiefly for the middle and larger ones—which is only broken up into the individual flagella at its extremity. The outer flagella of the tuft are smaller and separate, and vibrate freely in the surrounding fluid medium. The united tuft, on the other hand, performs only occasionally lashing and jerking movements. In exhausted and dying specimens the cilia separate into confused tufts. The structure of the anterior end carrying the tuft of flagella is very peculiar. A round and somewhat dark body, the nucleus, is situated a short distance behind the cluster of cilia; it stains deeply with carmine, and gives the impression of a homogeneous plasmatic body in the living organism, but after treatment

with dilute acetic acid it appears as a vesicular nucleus, with a large and dark irregular sheath containing nucleoli.

The nucleus lies in a space which is remarkable for its clear and transparent nature; it occupies almost the entire breadth of the anterior extremity, but rapidly narrows as it passes backwards, and in large specimens it can usually be traced only as far as the centre of the body (fig. 21 a), whilst in smaller examples it extends almost to the hinder end of the body (fig. 21 b). In the larger specimens also a delicate transparent band runs along the middle line of the body to the posterior end as a prolongation of the anterior light space. Round this clear space at the anterior end, which is triangular when seen in optical section, is a thick envelope of a denser and darker plasma, which is tolerably sharply bounded off from the remaining protoplasm (fig. 21 *a*). The body, therefore—at least, in the larger individuals—is divided into two portions, of which the anterior is somewhat shorter than the posterior. After treatment with dilute acetic acid the two segments are sometimes very clearly separated from each other, whilst there appears between them a space filled with fluid brought about by the varying contraction due to coagulation.

The hinder and larger half of the organism consists of a transparent granular protoplasm. It encloses a larger or smaller number of granular contents, which, so far as the author can judge, consist chiefly of food particles. In the organisms examined this part of the body usually contained a number of very dark, round, or oval granules, of a high refractive index, closely packed together, such as exist in quantities in the intestine of the cockroach; they are probably starch granules, but they have not been examined chemically. Individuals are occasionally found, which are very much smaller, and are free from such granular contents. A protoplasmic thread was often seen at the posterior end, which trailed as a tail-like prolongation of the body substance. Sometimes, also, numerous bodies of a considerable size, like those within, adhered to the outside of the hinder end of the organism, giving rise to the supposition that the hinder end took part in some undefined way in the ingestion of food; and this is rendered more probable by the fact that the peculiarly constructed anterior end is always found to be entirely free from food contents. No contractile vacuole is discoverable. Vacuoles are only very rarely found in the substance of these organisms; the author has, himself, observed them in only two cases, in neither of which was

there any appearance of contraction. But little is known, and that not certainly, of the reproduction.

Individuals have been met with which were provided with two tufts of cilia instead of with one, and which exhibited all that peculiar arrangement under each of the tufts, which would be present in an ordinary individual. Such specimens were always very variable in form, at one time contracting themselves to such a degree that the two clusters of cilia stood close together, and again extended themselves till they were upon opposite ends of the body. From what is at present known as to the prelude to division amongst the Flagellata, we are led to believe that these forms are about to undergo fission. On the other hand, it may be argued that such forms have been watched for a long time without any further advance in the process of division being observable.

A considerable number of individuals were once seen whose posterior extremities were beset with small cilia, but it has not been decided whether these forms stood in any relation to the final state of division. Very large specimens measured about 0·03 mm.; but, as already noticed, there are remarkable differences in size, as is shown by the figures 21 a and 21 b.

Lophomonas striata, n. sp.?

The form to be described under this name (Plate vi, fig. 21 c d) is also found in the rectum of *Blatta orientalis*. This peculiar organism, in relation to its possession of a large anterior tuft of cilia, is closely allied to *Lophomonas blattarum*, and the finer details of structure are exactly the same as in the ordinary kind. The form of the body, however, is very different: it is usually elongated and spindle-shaped, whilst the anterior end, for the reception of the tuft of flagella, is somewhat sharply conical, in opposition to the usually broad end in *Lophomonas blattarum*. Only occasionally is there any important deviation from this form: the spindle, however, appears sometimes longer, at other times shorter. Once a small form was seen (fig. 21, c), which differed notably from the ordinary individuals in the possession of an oval rounded body. The length of the body is the same on the average as in *Lophomonas blattarum*, but it is usually somewhat greater in the elongated spindle forms. The comparatively stiff and unbending nature of the body protoplasm is very peculiar, in contrast with the transparent protoplasm of the forms hitherto described. A very typical spiral longitudinal banding is seen, it is sometimes regular, at other times irregular,

even to confusion. It is absolutely peculiar in that the protoplasm is surrounded by many bands of high refractive index, of somewhat irregular outline. It is clear that it is not dependent on a spirally ribbed sheath. Nothing at all can be made out in the body of the organism beyond this banding; there is no trace of any granular contents, or granular plasma, and no nucleus, with its peculiar arrangements, such as is found in this neighbourhood in *Lophomonas blattarum*. Once a clear spot like a vacuole was seen at the anterior end of a specimen. Dying specimens conduct themselves quite peculiarly, for in them the body becomes broken up into a heap of threads, since the banded structures become separated, and lie confusedly on each other. This phenomenon seems to show that the chief part of the body is made up of such threads, as all that was visible between these broken down masses of threads, were small, round, and pale granules. This species when fresh moves as rapidly and energetically by means of its tuft of cilia as the ordinary *Lophomonas blattarum*, but like the latter it dies after a short time in indifferent fluids. They are found more rarely than *Lophomonas blattarum*, but sometimes they are found together in the same animal. Leydig appears to have observed a species of this genus in *Gryllotalpa*.

Uvella, Ehrenberg ('Die Infusionsthiere als vollkommene organismen,' p. 19).

Uvella virescens (Bory), Ehrenberg (op. cit., p. 20, pl. i, fig. 26).

Uvella virescens, Dujardin ('Hist. Nat. des Infusoires,' Paris, 1841, p. 301).

Uvella virescens, Perty ('Zur kenntniss kleinster Lebensformen,' etc., p. 176, pl. xiv, fig. 1).

Uvella virescens, Fromentel ('Études sur les Microzoaires,' Paris, p. 238, pl. xxvi, fig. 7).

This commonly occurring form consists of spherical free-swimming colonies, the constituent individuals of which are united in the centre of the colony by their tapering posterior ends (fig. 22, *a*). They are not, however, connected below, and are not embedded in a common case. Each of the yellowish or yellowish-green individuals on that pole which is furthest away from the centre of the colony has two large flagella which arise close to each other. The number of individuals which unite to form a colony is very variable. Fig. 22, a shows such a colony composed of only a few individuals; for Ehrenberg has found as many as eighty in a

single colony. The yellowish-green colouration is dependent, as in other cases, upon the presence of two pigment discs, which are relatively not very thick, of which one occupies each lateral half of the body, lying close beneath the surface. Between the two discs is only a small space, which appears on closer inspection as a colourless transparent line running longitudinally. The pigment is, therefore, not present in the body-substance in a finely divided condition, as Stein has described in certain red and yellow Flagellata. The pigment discs of Uvella are remarkably distinct; after the death of the organism, when the body protoplasm swells up, and the whole body becomes rounded, the pigment discs undergo the same change, and ultimately shrinking together form irregular or roundish bodies (fig. 22, b and c). In the hinder end of the body, at the spot where the tapering gives rise to the colourless point, are found two small contractile vacuoles close to each other (fig. 22, a *v*), which contract alternately and reappear upon the same spot. A nucleus cannot be seen under the ordinary conditions, although it can be detected by staining. As demonstrated by Beale's carmine, it lies somewhat in the centre of the body between the two pigment discs, whilst the rest of the body remains quite uncoloured (*n* in fig. 22, b and c). The body protoplasm is generally filled either with fine or coarse granules in larger or smaller numbers; the anterior end alone often appears to be quite free from such granules, and is therefore transparent. Only a single stage in the process of fission has been observed (fig. 22, d), and it agrees with the usual mode followed by other Flagellata. The division occurs lengthwise, and then the flagella and contractile vacuoles increase in number, as do also the pigment discs (fig. 22, d).

Encystation has also been observed in Uvella; such encysted forms being often found on crushing a colony among normal organisms, and also lying free in the watch glass in which the Uvella has been kept. These forms consist of a delicate irregular outer coat, enclosing a thicker coat, which immediately surrounds the encysted body. Within the cyst lie the much contracted pigment discs.

Among the individuals forming the Uvella colony a small Flagellate is found so frequently as to be almost normal (fig. 22, *a*). This small organism is long and spindle-shaped, it possesses two flagella, and fixes itself with its flagella-bearing end—which is more pointed—towards the centre of the colony. It calls to mind *Chloragonium*

euchlorum, Ehrb., or, perhaps, with greater distinctness, the zoospores of Colacium described by Cienkowski.[1]

Uroglena, Ehrenberg ('Die Infusionsthiere als vollkommene organismen,' Leipzig, 1838, pp. 61, 62, pl. iii, fig. 11).

Uroglena volvox, Ehrenberg (loc. cit.).

These organisms have been found by the author in enormous numbers, chiefly in some small ponds near Frankfort-on-the-Main, but also in a pond in the Grand Ducal Park at Carlsruhe. They form large-sized colonies, which are generally spherical, but never so regularly spherical as in Volvox, since they generally have more or less irregular blunt corners, and often deep constrictions. The individuals are ranged close to each other (fig. 22 *a*), and are enclosed in a gelatinous covering; the author has not observed the tails described by Ehrenberg, but finds that the hinder extremities of the individuals are simply rounded, and that there is no junction between the individual organisms. It is not yet determined whether the spaces in the interior of the colony, which are not occupied by the organisms, are filled with the gelatinous covering, or with fluid; but the author is inclined to think the latter, since he has observed great numbers of diatoms and other foreign bodies moving freely in this position. The greatest length of a single individual is, on the average, 0·011 mm. Each individual bears two flagella peripherally, a large chief flagellum tapering gradually from its point of origin, and a small accessory flagellum near it, as in Dinobryon.

The eye spot is close to the base of these flagella: the author has only observed a single one, whilst Ehrenberg has seen three, the increased number being due to impending fission.

In the anterior half of the body of each individual are two yellowish-brown or greenish-brown pigment spots. Treatment with alcohol extracts the bright green chlorophyll colouring material from the pigment discs, just as in the case of diatoms. The contractile vacuoles (*c*) are present singly (fig. 23, *a*), they swell considerably during the systole, so that the body wall has a hernia-like protrusion it contracts rapidly and suddenly. The nucleus has been demonstrated by carmine staining, followed by treatment with glycerine containing hydrogen chloride. The process of reproduction has not yet been followed out.

[1] "Ueber Palmellaceen und einige Flagellaten," 'Arch. f. Mikr. Anat.,' Bd. vi, 1870, p. 427.

II. Protozoa Flagellata resembling Rhizopoda.

1. A Flagellate with nuclearia-like rhizopod condition.—This organism has been shortly described by Cienkowski[1] as *Ciliophrys infusionum;* it has been twice found under the same conditions in considerable numbers, viz. in pond water which had stood some time in the house and had become somewhat foul; in one case, in company with a large quantity of *Antophysa vegetans*, and many other Flagellata, such as are usually found in foul ditch water. The organism is tolerably large, 0·03 mm. in length, but varying considerably in size. It is considerably elongated (fig. 24, a), and is somewhat tapering anteriorly; the front end, which bears the flagellum, is somewhat sharply truncated. The posterior end is usually rounded, and is sometimes drawn out into a tail-like appendage. This, however, appears only to be the case when the organism is passing into its rhizopod condition. A nucleus and contractile vacuole, both in a constant position, are seen within the protoplasm, which is tolerably clear. The nucleus lies at the front of the body, close below the base of the flagellum; whilst the contractile vacuole is about the centre, or somewhat above it, close under the surface. Other vacuoles, which are not contractile, are usually found, and near them large dark granules, sometimes of a greenish colour; these can only be looked upon as ingested food materials. Many secretion-granules are also present, heaped together at the posterior end.

If a moderately active Flagellate of this form be kept under observation for some time, it will often be found that the movement becomes slower, whilst the circumference becomes irregular. Fine pseudopodia are gradually thrust out, and to the destruction of the flagellum the organism becomes converted into a rhizopod form (fig. 24 b).

In this condition it closely resembles Cienkowski's *Nuclearia simplex* in its rounded circumference, and its numerous radiating and delicate pseudopodia. It is probable, however, that this form is not identical with Nuclearia. Cienkowski has observed a change in the reverse way, viz. from a rhizopod condition into an actively moving flagellate state. This faculty is also possessed by the organism just described, for the pseudopodia are retracted together, and the body gradually begins to move backwards and forwards, the cause of such movement being indiscernible. Finally, when the

[1] 'Arch. f. Mikr. Anat.,' Bd. xii, p. 29.

movement has become more energetic, the organism increases in length, and the flagellum is distinctly seen at one end. No observations have been made as to the reproduction or encystation of this interesting form.

2. **Rhizopoda possessing flagella.**—Such organisms have been described by Claparède and Lachmann[1] under the name *Podostoma filigerum*, by F. E. Schulze[2] as *Mastigamœba aspera*, and by Carter. The author has repeatedly found in somewhat foul pond water, which has stood for a considerable time in a glass, an organism which is not identical with any of the forms described. It has the appearance of a small naked rhizopod, with delicate and somewhat branched pseudopodia, which are not numerous (Pl. vi, fig. 25.) The shape is naturally very variable; in a tolerably elongated form the length is 0·02 mm. The protoplasm appears to be very transparent, it is homogeneous, and it never contains many particles. Usually there are a number of constant vacuoles, some of which contain dark granules, the ingested food materials, and moreover, minute dark granules in large or smaller numbers. There is no differentiation into Ecto and Entoplasm. The pseudopodia are never very long, and are generally finely pointed; comparatively seldom they are branched so as to be forked or antennate. A contractile vacuole, and sometimes more than one, is present. The vesicular nucleus, with its contained inner bodies, is clearly visible. In some specimens it can be readily seen that the organisms possess a large flagellum. Relatively, this flagellum is the largest observed amongst the Flagellata, as it is sometimes eight or ten times longer than the body. It is very delicate, and either vibrates only at its outer extremity or lashes along its whole length. The movements which the flagellum sometimes executes in relation to the body are very peculiar. As the whole body consists of movable amœboid protoplasm, the place of insertion of the flagellum is naturally variable, and the flagellum is often seen slowly moving round the body, and finally, returning to its original position.

The movement is usually like that of a Rhizopod; sometimes the movements of the flagellum are energetic, and the organism then begins to move like a Flagellate, by help of its flagellum. In such a case the organism always assumes an elongated shape (fig. 25 *b*), and the flagellum is

[1] 'Études sur les Infusoires,' i, p. 441, pl. xxi, figs. 4—6.
[2] 'Arch. f. Mikr. Anat.,' Bd. xi, p. 583.

stretched far forwards from the pointed extremity of the body; the pseudopodia, however, are not retracted.

In this condition the nucleus is situated in the pointed anterior extremity from which spring the flagella. It is remarkable that after moving, at most for a short time, by means of its flagellum, the little organism returns to its creeping mode of life.[1]

Amœba Blattæ, n. sp. von Siebold.[2] The author has already[3] given an account of the peculiar appearances observed in the nuclei of *Amœba princeps*, showing that the number and size of the nuclei undergo great variations. The same changes have lately been found to occur in other Amœba.

The *Amœba blattæ* (Pl. vi, fig. 26) rivals in size the *Amœba princeps*, it is found as a parasite in the dilatation at the commencement of the rectum in the cockroach. In this situation it lives with *Oxyurus*, *Nyctotherus ovalis*, *Lophomonas*, and numberless small Flagellata. On making a preparation to show the living entoparasitic Amœbæ contained in this position, they may be seen as round, and apparently lifeless masses, which soon exhibit their somewhat sluggish movements, thereby declaring their true nature. The protoplasm of this species appears to be neither homogeneous, alveolar, nor reticular, as in many other Protozoa, but always very markedly fibrillar. On close investigation it may be noticed that it appears to be made up of numerous dark threads, which are somewhat irregular, and are occasionally knotted or granular. These threads either run more or less regularly in reference to the direction of movement of the body, or they cross it somewhat confusedly. A clear intermediate mass separates individual threads from each other: from its refractive index, and its feeble reddish-colour, this mass appears to be fluid. A peculiar homogeneous outer layer, the ectoplasm, such as is often found in Amœbæ, and amœboid organisms, is not here normally present. The contour of the body is formed by a layer of dense protoplasm, which is usually very delicate; from this layer arise the protoplasmic threads of the body, and with it they are in direct continuity. This dense surface layer of protoplasm is often heaped up at certain spots in the body into great masses (fig. 26 a), in which case it is seen as

[1] "On Free-swimming Amœbæ," see also Cienkowski, 'Pringsh. Jhrb. f. w.,' Bd. iii, p. 434, and Tatem, 'Month. Micr. Journ.,' i, p. 352.

[2] 'Beiträge zur kenntniss Wirbelloser Thiere,' Danzig, 1839, p. 69.

[3] 'Studien über die ersten Entwickelungs-orgänge,' etc., p. 164.

a homogeneous mass of tolerably high refractive index. The author then goes on to describe the way in which these masses are produced by the various movements of the protoplasm. The filiform structure of the Amœba disappears after the application of such pressure to the cover glass as will kill the organism, at the same time the protoplasm becomes homogeneous. This phenomenon is due, the author states, to the fact that the threads of protoplasm swell up under the pressure, take up the fluid, and fuse with one another. In this Amœba, the protoplasm on the surface of the body sometimes becomes homogeneous during the execution of moderately active movements, sometimes travelling over the surface as a hyaline seam of greater or less extent, whilst sometimes short and bluntly conical pseudopodia arise. The formation of such pseudopodia, however, is rare.

Inside the body are the food particles in greater or less numbers, the nature of which has not yet been made out. Contractile vacuoles have been several times observed, they were numerous, and arose upon the surface of the body in a semicircle, uniting at the period of contraction.

The nucleus is usually large and oval, 0·018—0·02 mm. in diameter in a moderately large specimen (fig. 26, a, *n*). It consists of a very large thick and dark case which is apparently homogeneous (fig. 26, b, *h*). Within this case are finely granular, reticulated contents, which surround a sheath probably filled with fluid. Within this sheath a dark corpuscle is sometimes seen, and round it is a delicate membrane. It is remarkable that these nuclei often appear distinctly pointed at one end, or have a neck or knob-like prominence (fig. 26 *c*), a peculiarity which, so far as the author knows, has not yet been observed in any other nucleus. Occasionally two nuclei are found in a single individual, but this frequently happens in other Amœbæ. There has also been found an individual with four round nuclei of the same size, 0·0086 mm.; further, one with eight nuclei, 0·007—0·0086 mm.; and one with fourteen nuclei, 0·006—0·0072 mm. These individuals with numerous nuclei are not so large as the organisms with one or two nuclei. The smaller nuclei were spherical, as is the case with the smaller nuclei in *Amœba princeps*. Two examples were found with numerous nuclei, the one with six, the other with nine, in which some of the nuclei departed from the round form. In the first example three of the nuclei were irregularly elongated, whilst in the second, seven were drawn out into spindles. The small nuclei differ in their construction from the large ones, in that the space filled with fluid is in the

former, very large, so that the peculiar contents of the nuclei are bounded by a proportionally delicate sheath.

Near these moving Amœbæ tolerably large cysts are frequently found; they undoubtedly take part in the reproductive process of these organisms. The cysts (fig. 26 d) are always quite round, with a tolerably delicate sheath lying close to the contents. The diameter is somewhat variable, usually about 0·03—0·04 mm., and in one case 0·007 mm. The protoplasmic body contained in the sheath always consists in part of a very clear and quite homogeneous protoplasm, and in part of a very finely granular protoplasm. Inside the cyst a number of nuclei are invariably found, they are of the same nature as the smaller nuclei in the ordinary Amœba condition. The author has counted 11, 19, and occasionally 25 or even 30 small nuclei. The size of these nuclei varies somewhat in one and the same cyst, so that the measurements taken vary between 0·003—0·008 mm. The investigations which have been as yet made do not afford any clear evidence of the relationship of the single to the multi-nucleated condition.

On the Morphology *and* Systematic Position *of the* Spongida. By F. M. Balfour, M.A., Fellow of Trinity College, Cambridge.

Professor Schulze's[1] last memoir on the development of Calcareous Sponges, confirms and enlarges Metschnikoff's[2] earlier observations, and gives us at last a fairly complete history of the development of one form of Calcareous Sponge. The facts which have been thus established have suggested to me a view of the morphology and systematic position of the Spongida, somewhat different to that now usually entertained. In bringing forward this view, I would have it understood that it does not claim to be more than a mere suggestion, which if it serves no other function may, perhaps, be of use in stimulating research.

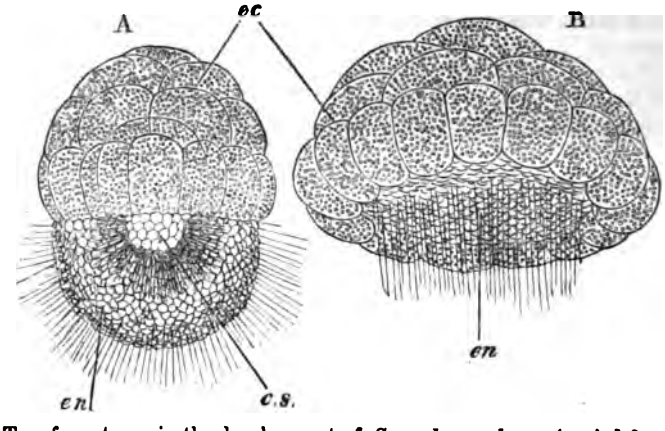
To render clear what I have to say, I commence with a very brief statement of the facts which may be considered as established with reference to the development of *Sycandra raphanus*

[1] "Untersuchungen über d. Bau u. d. Entwickelung der Spongien," 'Zeit. f. wiss. Zool.,' Bd. xxxi, 1878.

[2] "Zur Entwickelungsgeschichte der Kalkschwamme," 'Zeit. f. wiss Zool.,' Bd. xxiv, 1874.

the form which was studied by both Metschnikoff and Schulze. The segmentation of the ovum, though in many ways remarkable, is of no importance for my present purpose, and I take up the development at the close of the segmentation, while the embryo is still encapsuled in the parental tissues. It is at this stage lens-shaped, with a central segmentation cavity. An equatorial plane divides it into two parts, which have equal shares in bounding the segmentation cavity. One of these halves is formed of about thirty-two large, round, granular cells, the other of a larger number of ciliated clear columnar cells. While the embryo is still encapsuled a partial invagination of the granular cells takes place, reducing the segmentation cavity to a mere slit; this invagination is, however, quite temporary and unimportant, and on the embryo becoming free, which shortly takes place, no trace of it is visible; but, on the contrary, the segmentation cavity becomes larger, and the granular cells project very much more prominently than in the encapsuled state.

FIG. 1.



Two free stages in the development of *Sycandra raphanus* (copied from Schulze).

A. Amphiblastula stage; B, a later stage after the ciliated cells have commenced to become invaginated; *cs.* segmentation cavity; *ec.* granular cells which will form the ectoderm; *en.* ciliated cells which become invaginated to form the entoderm.

The larva, after it has left the parental tissues, has an oval form and is transversely divided into two areas (fig. 1, A). One of these areas is formed of the elongated, clear, ciliated cells, with a small amount of pigment near the inner ends (*en*), and the other and larger area of the thirty-two granular cells already mentioned (*ec*). Fifteen or sixteen of these are arranged as a special ring on

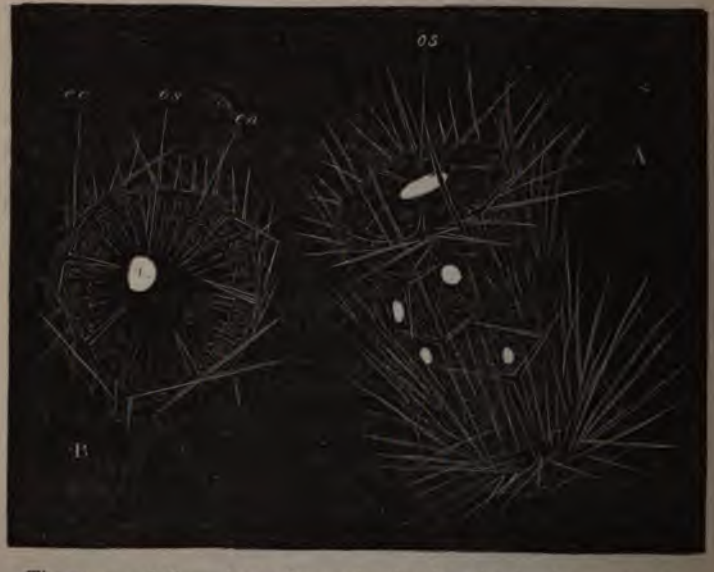
the border of the clear cells. In the centre of the embryo is a segmentation cavity (*cs*) which lies between the granular and the clear cells, but is mainly bounded by the vaulted inner surface of the latter. This stage is known as the amphiblastula stage. After the larva has for some time enjoyed a free existence, a remarkable series of changes takes place, which result in the invagination of the half of it formed of the clear cells, and form a prelude to the permanent attachment of the larva. The entire process of invagination is completed in about half an hour. The whole embryo first becomes flattened, but especially the ciliated half which gradually becomes less prominent (fig. 1, B), and still later the cells composing it undergo a true process of invagination. As a result of this invagination the segmentation cavity is obliterated and the larva assumes a compressed plano-convex form with a central gastrula cavity, and a blastopore in the middle of the flattened surface. The two layers of the gastrula may now be spoken of as ectoderm and entoderm. The blastopore becomes gradually narrowed by the growth over it of the outer row of granular cells. When it has become very small the attachment of the larva takes place by the flat surface where the blastopore is situated. It is effected by protoplasmic processes of the outer ring of ectoderm cells, which, together with the other ectoderm cells, now become amœboid. At the same time they become clearer and permit a view of the interior of the gastrula. Between the ectoderm cells and the entoderm cells which line the gastrula cavity there arises a hyaline structureless layer, which is more closely attached to the ectoderm than to the entoderm, and is probably derived from the former. A view of the gastrula stage after the larva has become fixed is given in fig. 2.

FIG. 2.

Fixed Gastrula stage of *Sycandra raphanus* (copied from Schulze). The figure shows the amœboid ectoderm cells (*ec*) derived from the granular cells of the earlier stage, and the columnar entoderm cells, lining the gastrula cavity, derived from the ciliated cells of the earlier stage. The larva is fixed by the amœboid cells on the side on which the blastopore is situated.

After invagination the cilia of the entoderm cells can no longer be seen, and are probably absorbed, and their disappearance is nearly coincident with the complete obliteration of the blastopore, an event which takes place shortly after the attachment of the larva. After the formation of the structureless layer between the ectoderm and entoderm, calcareous spicules make their apppearance in it as delicate unbranched rods pointed at both extremities. The larva when once fixed rapidly grows in length and assumes a cylindrical form (fig. 3, A). The sides of the cylinder are beset with calcareous spicules which project beyond the surface, and in addition to the unbranched forms, spicules are developed with three and four rays as well as some with a blunt extremity and serrated edge. The extremity of the cylinder opposite the attached surface is flattened, and though surrounded by a ring of four-rayed spicules is itself free from them. At this extremity a small perforation is formed leading into the gastric cavity which rapidly increases in size and forms an exhalent osculum (*os*). A series of inhalent apertures are also formed at the sides of the cylinder.

FIG. 3.



The young of *Sycandra raphanus* shortly after the development of the *Spicula* (copied from Schulze).

A. View from the side; B, view from the free extremity; *os.* osculum; *ec.* ectoderm; *en.* entoderm composed of collared ciliated cells. The terminal osculum and lateral pores are represented as oval white spaces.

The relative times of appearance of the single osculum and smaller apertures is not constant for the different larvæ. On the central gastrula cavity of the sponge becoming placed in communication with the external water, the entoderm cells lining it become ciliated afresh (fig. 3, B, *en*) and develop the peculiar collar characteristic of the entoderm cells of the Spongida. When this stage of development is reached we have a fully developed sponge of the type made known by Hæckel as Olynthus.

Till the complete development of other forms of Spongida has been worked out it is not possible to feel sure how far the phenomena observable in Sycandra hold good in all cases. Quite recently the Russian embryologist, M. Ganin,[1] has given an account, without illustrations, of the development of *Spongilla fluviatilis*, which does not appear reconcilable with that of Sycandra. Considering the difficulties of observation it appears better to assume for this and some other descriptions that the observations are in error rather than that there is a fundamental want of uniformity in development amongst the Spongida.

The first point in the development of Sycandra which deserves notice is the character of the free swimming larva. The peculiar larval form, with one half of the body composed of amœboid granular cells, and the other of clear ciliated cells is nearly constant amongst the Calcispongiæ, and widely distributed in a somewhat modified condition amongst the Fibrospongiæ and Myxospongiæ. Does this larva retain the characters of an ancestral type of the Spongida, and if so what does its form mean? It is, of course, possible that it has no ancestral meaning but has been secondarily acquired; I prefer myself to think that this is not the case, more especially as it appears to me that the characters of the larva may be plausibly explained by regarding it as a transitional form between the Protozoa and Metazoa. According to this view the larva is to be considered as a colony of Protozoa, one half of the individuals of which have become differentiated into nutritive forms, and the other half into locomotor and respiratory forms. The granular amœboid cells represent the nutritive forms, and the ciliated cells represent the locomotor and respiratory forms. That the passage from the Protozoa to the Metazoa may have been effected by such a differentiation is not improbable on *à priori* grounds, and fits in very well with the condition of the free swimming larva of Spongida, though another and perhaps equally plausible suggestion as to this passage has been put forward by my friend Professor Lankester.[2]

[1] "Zur Entwickelung d. Spongilla fluviatilis," 'Zoologischer Anzeiger,' vol. i, No. 9, 1878.

[2] "Notes on Embryology and Classification." This Journal, Vol. XVII,

While the above view seems fairly satisfactory for the free swimming stage of the larval Sponge there arises in the subsequent development a difficulty which appears at first sight fatal to it. This difficulty is the invagination of the ciliated cells instead of the granular ones. If the granular cells represent the nutritive individuals of the colony, they and not the ciliated cells ought most certainly to give rise to the lining of the gastrula cavity, according to the generally accepted views of the morphology of the Spongida. The suggestion which I would venture to put forward in explanation of this paradox involves a completely new view of the nature and functions of the germinal layers of adult Sponges.

It is as follows :—When the free swimming ancestor of the Spongida became fixed, the ciliated cells by which its movements used to be effected must have to a great extent become functionless. At the same time the amœboid nutritive cells would need to expose as large a surface as possible. In these two considerations there may, perhaps, be found a sufficient explanation of the invagination of the ciliated cells, and the growth of the amœboid cells over them. Though respiration was, no doubt, mainly effected by the ciliated cells, it is improbable that it was completely localized in them, but the continuation of their function was provided for by the formation of an osculum and pores. The ciliated collared cells which line the ciliated chambers, or in some cases the radial tubes, are undoubtedly derived from the invaginated cells, and if there is any truth in the above suggestion, the collared cells in the adult Sponge must be mainly respiratory and not digestive in function, while the normal epithelial cells which cover the surface of the sponge, and in most cases line the greater part of the passages through its substance, must carry on the digestion.[1] If the reverse is the case the whole theory falls to the ground. It has not, so far as I know, been definitely made out where the digestion is carried on. Lieberkühn would appear to hold the view that the amœboid lining cells of the passages are mainly concerned with digestion, while Carter holds that digestion is carried on by the collared cells of the ciliated chambers.

1877. It seems not impossible, if the speculations in this paper have any foundation that while the views here put forward as to the passage from the Protozoon to the Metazoon condition may hold true for the Spongida, some other mode of passage may have taken place in the case of the other Metazoa.

[1] That the flat cells which line the greater part of the passages of most Sponges are really derived from ectodermic invaginations appears to me clearly proved by Schulze's and Barrois' observations on the young fixed stages of Halisarca. Ganin appears, however, to maintain a contrary view for Spongilla.

If it is eventually proved by actual experiments on the nutrition of Sponges, that digestion is carried on by the general cells lining the passages, and not by the ciliated cells, it is clear that neither the ectoderm nor entoderm of Sponges will correspond with the similarly named layers in the Cœlenterata and the Metozoa. The invaginated entoderm will be the respiratory layer and the ectoderm the digestive and sensory layer; the sensory function being probably mainly localised in the epithelium on the surface, and the digestive one in the epithelium lining the passages. Such a fundamental difference in the germinal layers between the Spongida and the other Metazoa, would necessarily involve the creation of a special division of the Metozoa for the reception of the former group.

Flagellated Organisms *in the* Blood *of* Healthy Rats.[1]

By Timothy Richards Lewis, M.B.

It will be recollected that it is one of the fundamental tenets of M. Pasteur's creed that neither microscopic organisms nor their germs are ever found in the blood of an animal in health. Doubtless our conception of what implies good health may differ, and especially so when it is the health of an animal, and not of a person, that may be the subject of debate. If it be maintained that an animal affected with either epiphytes or entophytes, with epizoa or entozoa, is not in the enjoyment of full health, then there can be but few perfectly healthy animals. The organs of some animals are almost never absolutely free from parasites. It would nevertheless be scarcely justifiable to pronounce such animals as diseased in the ordinary sense.

So much being admitted, it is scarcely possible that this portion of M. Pasteur's doctrine can be correct. For some years past I have taken considerable interest in this matter, and my attention was drawn to it in a special manner in May last year, by my having been directed by the Government to make inquiries regarding the spirillum of Bombay-fever. Whilst doing this I had occasion to examine the blood of a considerable number of animals, and eventually (July, 1877) detected organisms in

[1] This chapter forms a portion of a paper on "The Microscopic Organisms found in the Blood of Man and Animals," which will shortly be published in the 'Fourteenth Annual Report of the Sanitary Commissioner with the Government of India.' Another portion of this paper, "The Nematoid Hæmatozoa of Man," will appear in the next number of this Journal.—Ed.

the blood of a rat which, at first sight, I took to be of the nature either of vibrions or spirilla. The blood when transferred to the microscope appeared to quiver with life, but for some considerable time nothing could be detected to account for this animated condition, as the blood-corpuscles were somewhat closely packed. On diluting the blood with a half per cent. solution of salt, motile filaments could be seen rushing through the serum, and tossing the blood-corpuscles about in all directions. Their movements were of a more undulatory character than are the movements of spirilla, and the filaments were thicker, more of a vibrionic aspect. They were pale, translucent beings, without any trace of visible structure or granularity; but, as their movements were so rapid, exact information as to their microscopical characters could not be ascertained at the time. The slides were therefore placed under a bell-glass until these should diminish.

On the following morning the activity of the filaments was much less. Their movements were more restricted and more undulatory in character, and the blood-corpuscles, having become somewhat agglutinated, had apparently squeezed out the organisms, so that the latter occupied the serum-areas of the preparations. After watching their movements for some time under a Hartnack's No. 9 immersion objective, it was observed that every now and then blood-corpuscles, some considerable distance from any visible motile filament would suddenly quiver. On carefully arranging the light it was eventually observed that this movement was due to the existence of a very long and exceedingly fine flagellum, apparently a posterior flagellum, as the organisms seemed, generally, to move with the thicker end forwards—the flagellum being seen following it, and lashing the fluid during the moment it remained in focus. I have not been able to detect any flagellum at the opposite end. The greater number of the figures reproduced in the woodcut represent these organisms as they are observed a few hours after the blood has been obtained, when their movements are not so rapid, and the flagellum becomes recognisable. They may sometimes be kept alive for two or three days, but generally the greater portion will have died within twelve or twenty-four hours; and not only have died, but also disappeared from view.

When very carefully watched, the plasma constituting the thicker portion of their substance may be seen suddenly to swell out at certain places—sometimes so as to divide the "body" into two parts, as shown in the middle figure; at other times two or three such constrictions and dilatations may be detected, the dilatations being, possibly, observable only on one side. At other times they assume an arrow-shaped aspect, as shown in the

lowest figure. Occasionally something like granularity may be observed before their disappearance, but not a trace of them is left after their disintegration. It seems as though they had been dissolved in the serum in which they were found.

Flagellated organisms in the blood of healthy rats. A few red blood-corpuscles and one white corpuscle are included in the figure. Magnified 700 diameters.

They may readily be preserved by spreading out a thin layer of the blood containing them over a thin covering-glass and inverting it over a weak solution of osmic acid. The preparation should be removed as soon as it presents a dry, glazed appearance, and may be thus mounted in the dried condition or in a saturated solution of acetate of potash. I have, however, never been able to detect the flagellum in such a preparation; apparently the refractive index of the substance forming the flagellum and that of the serum approximates so closely that the last can only be detected when creating a current by its movements. The "body" remains nearly as translucent after the action of the osmic acid fumes as it was in the living condition, so that the presence of the protozoa in such a preparation may readily be overlooked, owing to the absence of any movements to direct attention to them.

When, however, a preparation of blood of this kind is dried in the manner ordinarily suggested for preserving specimens of blood, and especially if a little of a weak solution of aniline blue be afterwards poured over the dried slide, the body of the protozoon will present a very different appearance. It will be found to have contracted irregularly, and to manifest a somewhat granular and *shreddy* appearance, suggestive of a coagulated, fibro-albuminous substance. The "body" portion becomes flattened towards its middle to double its original width, and both ends become almost acutely pointed. The flagellum part is only visible for about half its true length, and this portion of it appears to consist of the same substance as the body. Possibly the now invisible portion of the flagellum may consist of a

substance slightly different from that of the body; or may have been retracted during the drying. I have prepared micro-photographs of slides prepared in both ways,[1] hoping that possibly an image of the entire lash might thus be obtained, even though the eye could not distinguish any, but have not succeeded, notwithstanding that the rays of light were caused to pass through glass of various colours. The logwood solution recommended by Koch for this purpose also failed in my hands.

It is not possible to secure accurate measurements of these organisms during the period of inactivity, nor of the lash at any time, seeing that the latter becomes for the most part invisible in preserved preparations. The body-portion, however, may readily be measured after they have been killed by means of osmic acid. The width of the anterior half, or body-portion, averages ·8 to 1μ, or precisely that of ordinary blood-bacilli, and its length from 20 to 30μ, or an average of 25μ. The flagellum, so much of it as is visible, is somewhat of the same length, so that the total length of the organism equals about 50μ, or about $_{\frac{1}{0}\frac{1}{0}}$". The lash, however, may be considerably longer than this, as the slope from the body-portion is very gradual, and when the eye follows it to the bounds of visibility an impression is conveyed that there may be still more of it, beyond the power of either Ross' $\frac{1}{12}$" or Powell and Lealand's $\frac{1}{16}$" to reveal.

They are not very sensitive to the action of reagents; a weak solution of ammonia did not affect them for some time, but a stronger solution of potash affected such of them as it came into contact with at once: others in the middle of the field continued to exhibit movements for several hours; probably they had not been touched by the potash. A weak solution of bichloride of mercury in acetate of potash and camphor water (as used for preserving preparations) did not seem to affect them materially, seeing that they maintained their activity in such a solution for eight hours. They retain their vitality longer in a weak salt-solution than in pure distilled water. A cover-glass with an aqueous solution containing them was inverted over a bottle of chloroform for several minutes, but the movements of the organisms were unaffected; if, however, a drop of blood containing them be similarly placed over chloroform they disappear, probably owing to the action of the chloroform-vapour on the blood itself.

A drop of the blood was placed on a slide arranged for the

[1] Two such illustrations have been reproduced by the permanent photographic process of the Autotype Company, and will be issued with the complete paper in the Government of India Sanitary Report already referred to.

application of electricity to microscopic preparations, and it was found that an interrupted current of such a strength as could not be comfortably borne by an individual was tolerated by these beings for several consecutive hours. The only difference appreciable between a preparation thus dealt with and one not so treated was, that the movements ceased a few hours sooner in the former than in the latter, possibly owing to the chemical change induced in the blood itself by the current.

I have examined the blood of a great number of rats for the purpose of ascertaining what proportion of them contains these organisms in their blood, and find that of those specially examined for this purpose their existence was demonstrated in 29 per cent. Sometimes, however, the number detected were very few, not more than one or two in a slide, but in the greater number of cases they were very numerous, every slide containing several hundreds.

Being anxious to ascertain precisely the species of rats in which these organisms were found, I consulted an accomplished naturalist, Dr. John Anderson, Superintendent of the Indian Museum, and he was so good as to identify the specimens for me from time to time. The result has been that it has been definately ascertained that these organisms may be found in two species, viz. *Mus decumanus* and *Mus rufescens*.

It would appear that they are not found in mice. I have examined the blood of a large number, but never detected any organisms of the kind; nor have I seen them in any animals other than rats.

It is possible that these minute organisms ought to have been described in the part of this paper devoted to the description of microphytes, as they present many features in common with motile organisms undoubtedly of vegetable origin: on the other hand, taken as a whole they appear to approach more closely to the forms of life usually classified as Protozoa; such, for example, as several of the species of Dujardin's genus *Cercomonas*. It should, however, be noted that many believe that these organisms are zoospores and not animalcules.

The nearest approach to a description of these hæmatozoa which I can find is in a recent paper by Bütschli,[1] in which he refers to a flagellated parasite which he has often observed in the intestinal canal of a free nematode (*Trilobus gracilis*). He refrains from giving it a name, owing to the uncertainty which exists with regard to organisms of this kind. He generally found them in large numbers, often forming stellate colonies owing to their being attached by their non-flagellated ends. They readily became detached, and then presented a some-

[1] See page 68 and Plate VI, fig. 5, of the present number of this Journal.

what spindle-shaped body, about 11μ in length, and with a somewhat thick flagellum about double this length, so that the total length of the protozoon would be 33μ, something more than half the length of the flagellated organism found in the rat's blood. Near the base of the flagellum of Bütschli's protozoon a contractile vacuole could be distinguished, but I have not been able to detect any such vacuole in these rat-hæmatozoa.

Seeing that the blood of such a large proportion of rats contains these organisms, I can hardly suppose that their existence has hitherto escaped notice, unless it be that rats in Europe do uot barbour like parasites. Davaine,[1] in the recent edition of his work, makes mention that M. Chaussat had found minute nematodes in the blood of a black rat (*Mus rattus*), but I have not seen any nematode in the blood of rats in this country. In the tissues, bladder, &c., of rats such parasites are very common, but their description does not come within the province of this paper.

The nearest approach to the flagellated hæmatozoa of rats which I have seen described is to be found in a foot-note in Dr. Bastian's 'Beginnings of Life,'[2] where it is stated that Dr. Gros had seen minute worms (*vermicules*) in the blood of a field-mouse (*mulot*) which were so numerous as to cause the blood to present an animated appearance; and that the blood of the mole was often found to be in a similar condition. They were so small as to be barely visible under a power magnifying 400 diameters. I have not been able to obtain any minute description of these *vermicules*, but I anticipate that it will be found that they closely resemble the flagellated protozoa found in the blood of Indian rats.

With regard to the health of the rats in which these flagellated organisms were detected, there was nothing to suggest in any way that they were less healthy than others not so affected, and I have repeatedly kept rats for a considerable time for the purpose of observing whether any special symptoms would be manifested suggestive of the existence of such organisms in the circulation. It should be mentioned that it frequently happened that the rats caught in a particular room would be affected, whereas the blood of rats in another part of the building would not contain them. The servants had ultimately come to recognize this, as, whenever they learnt that a particular rat's blood contained the desired organisms, they diligently endeavoured to secure the rest of the family.

Calcutta, August, 1878.

[1] 'Traité des Entozoaires,' Edit. ii, pp. 11, 957; 1877. Leuckart's 'Parasiten,' vol. ii, p. 636.

[2] Vol. ii, p. 338; 1872.

NOTES AND MEMORANDA.

Observations on the Capitellidæ by Dr. Hugo Eisig.—A peculiar organ connected with the alimentary tract of the Capitellidæ has recently been described by Dr. Hugo Eisig, under the title Nebendarm ("Nebendarm d. Capitellidæ," 'Zoologischer Anzeiger,' No. 7, 1878). This organ, which has been met with in all the main families of the Capitellidæ, consists of a narrow tube on the neural side of the alimentary tract into which it opens in front and probably also behind. The anterior opening is situated close to the posterior boundary of the œsophagus. The position of the posterior opening varies somewhat, and its existence has not been so clearly established as that of the anterior opening. The chief interest connected with this organ is the comparison Dr. Eisig has made on the one hand between it and an embryonic organ found in the Ichthyopsida, and named subnotochordal rod, and on the other with the siphon of the Echinoid alimentary tract. The subnotochordal rod is primitively a canal split off from the neural side of the alimentary tract for the greater part of its length, which soon becomes solid, and occupies a position (according to Dr. Dohrn's view of the relationship between Annelida and Vertebrata) very similar to that of the Nebendarm of the Capitellidæ. The siphon of the Echinoids resembles the Nebendarm in communicating at both extremities with the alimentary tract. Dr. Eisig mentions that Spengel has recently detected in Bonellia an organ similar to the Nebendarm in its connections. The homologies suggested by Dr. Eisig for the peculiar organ he has discovered are certainly plausible, but can hardly claim to be satisfactorily established.

The segmental organs of the Capitellidæ have also been studied by Dr. Eisig ('Mittheilungen a. d. Zoologischen Station zu Neapel.', Bd. I, Heft I), and the conclusions he has arrived at are of some interest in relation to the possible homology between the vertebrate segmental tubes and the segmental

organs of the Annelida. It is generally stated that in no case is there more than one pair of segmental organs in each annelidan segment, although the coexistence of segmental organs and generative ducts in the same segment in the Terricolus Oligochæta led Professor Lankester to regard two as the typical number of pairs for each segment. Dr. Eisig has now shown that in Notomastus more than one pair of segmental organs is frequently present in a segment, and that in *Capitella capitata* a plurality of these organs in each segment is the rule.

Moreover, in Capitella the number in each segment increases from before backwards. In adult Amphibia there are usually several segmental tubes in each segment, and the actual number in each segment also increases from before backwards. This fact has been used as an argument against the comparison of the segmental organs in Vertebrata and Annelida; but Dr. Eisig's observations prove that on this point at any rate there is no important difference between the organs in the two types.—F. M. B.

Bacteria as the Cause of the Ropy Change of Beet-root Sugar.—The so-called "Frog-spawn" of sugar manufacturers is a gelatinous formation, the origin of which has hitherto been explained in various ways. Professor Cienkowski has recently published at Charkow a memoir, in which he describes and figures a Bacterium as the cause of the remarkable and economically important phenomena connected with this alteration of sugar. According to Scheibler, the "Frog-spawn" is the protoplasm of the cells of the sugar-beet; according to Jubert and Mendes, this gummy substance is an aggregate of various organised ferments. Durin ascribes the "Frog-spawn" to a peculiar fermentation, due to the action of diastase on crystalline sugar, whereby the latter is broken up into cellulose (the spawn) and glucose.

Cienkowski's researches, carried on both in a sugar factory and by means of culture experiments, prove that the view put forward by Jubert and Mendes is essentially the correct one; the "Frog-spawn" is in reality a product of the vital activity of Bacteria; it is to these organisms, and not to diastase, that we must ascribe the decomposition of the crystalline sugar discovered by Durin.

The jelly of the "Frog-spawn" shows in its structure and development the closest resemblance to the *Ascococcus Billrothii* of Cohn (see this Journal, vol. XVI, p. 264, and Plate XX, fig. 1, for Cohn's description and figure of *Ascococcus Billrothii*). It is, perhaps, only a variety of that species, and in any case belongs

to the same genus of Schizophyta, and may be named "*A. mesenteroides.*"

A structure identical in every respect with the "Frog-spawn" of sugar factories arises spontaneously on slices of cooked beet-root which are kept moist with free access of air; such culture specimens differ from those of the factories only in their smaller size and less density of the jelly. The jelly-balls of the "Frog-spawn" consist of accumulations of jelly-masses or units, the so-called "Gallertkerne." These units are naked, without envelope; they are closely adpressed one to another, or are attached to one another in rows so as to form botryoidal loose or compact gut-like masses. By combination of such units spherical or irregularly-shaped lumps are produced, which again become compacted into larger masses. The jelly of the ultimate spheroids has a varying consistence—hard, elastic, sharply defined, or semi-fluid, with confluent outlines. It is soluble in concentrated potassic hydrate and in sulphuric acid; according to Durin, also in ammonio-cupric hydrate. Cienkowski failed to obtain this reaction, and only saw a faint blue coloration as the result of this reagent. Iodine with strong sulphuric acid produces no change in the jelly.

The most important part of the ultimate spheroids are the builders of the jelly—namely, the Bacteria embedded in it. In young examples they are present without exception; in older lumps difficult to detect. They exhibit the most varied forms, which are commonly known as Micrococcus, Torula, Bacterium-chains, Bacillus, and Vibrio. The common Bacteria pass into the Zoogloea condition, developing from colourless Leptothrix-like filaments (see this Journal, October, 1878) by a process of transverse subdivision and by the production of jelly around *both entire filaments* and the pieces into which they subdivide, and we find that the developmental history of the "Frog-spawn" is similar. Here too, as forerunners of the gelatinous growth, we find colourless filaments, which are often serpentine in form. The gelatinization of the Ascococcus-builders is easy to follow, especially when they are growing on very slimy substrata. But the "Frog-spawn" will also originate directly around isolated Bacteria. Such gelatinous ultimate spheroids, formed independently of one another come into contact with one another by further growth, adhere together and form miniature examples of the "Frog-spawn." The nearly allied *A. Billrothii* develops itself spontaneously on cooked and uncooked beet-root. The jelly which envelopes the Bacteria is in this case not so copious, and less refringent, than in the former species. In cultures kept fairly dry *A. Billrothii* attains an enormous size; it is easily visible with the naked eye. It forms brown or greenish heaps

composed of numerous upgrowths; such examples differ in many respects from the forms described by Cohn and Billroth. The ultimate morphological elements into which they can be divided are, as in the former species, gelatinous spheroids with enclosed Bacteria.

All the properties of the "Frog-spawn," and nearly all the phenomena which accompany its formation, are in harmony with the supposition that these jelly-masses of the sugar factories are produced by Bacteria. Only in the extraordinary rapidity of their production (half an hour according to Feltz), do we come upon a difficulty, the explanation of which can only be looked for when we have a fuller knowledge of the developmental history of Bacteria. As a starting-point for further researches in this direction the following facts are of value:

(1) That in very viscid saccharine solutions all the Bacteria, without forming individualised Zoogloœa-masses, are embedded in a common gelatinous substance which is coagulated by alcohol. (2) The capability possessed by the Bacteria of forming balls of this substance around themselves. (3) That a mechanical movement of the nutrient fluid appears to act favorably on the formation of the ball-like masses. A very viscid decoction of beet takes, as Cienkowski says he has often seen, a marked gelatinous consistence almost immediately when agitated. The mechanical movement of the beet-juice during the process of squeezing it out of the roots, will probably enough prove in this way to be one of the essential conditions of the rapid formation of "Frog-spawn."

Cienkowski's observations show then, that the "Frog-spawn" of the sugar-factories is no peculiar isolated phenomenon, but without any difficulty can be assigned a place in the category of the processes of jelly-formation so widely spread among the Algæ. —E. Ray Lankester.

Stein's 'Organismus der Infusionsthiere.'—The first volume of the third part of this great work has just appeared, consisting of 150 pages of letterpress and 24 folio plates. The third part is devoted to the Flagellata, and in the present volume we have an exhaustive history of the discoveries and writings of previous observers, from Ehrenberg to Carter, Busk, Williamson, Hicks, and James-Clarke. The plates are accompanied by full explanations; the systematic description of genera and species will follow. Forms allied to those described in Professor Bütschli's paper, an abridged translation of which appears in the present number of this Journal, are figured in profusion. A most remarkable form is the *Rhipidodendron splendidum*, a tube-making Flagellate, the tubes of which are aggregated in dense

flabelliform masses. The genera Volvox, Pandorina, Chlamydococcus, &c., as well as Euglena and Phacus, are included by the author among the animal Flagellata, and are copiously illustrated. The antherozooids of Volvox are regarded merely as a smaller generation of Flagellate individuals. The Ritter von Stein regards this as probably the most interesting and important section of his great work, and all will agree that its appearance is most opportune.

PROCEEDINGS OF SOCIETIES.

Dublin Microscopical Club.

11*th April*, 1878.

Peronospora infestans ravages, exhibited.—Dr. Moore showed some of the leaf-tissue of the potato permeated by the Peronospora-pest, in order to point out the manner in which it became thereby disintegrated and killed.

Dinophysis norvegica, from Melville Bay, was exhibited by Dr. Moss, R.N.

Biddulphia Chinensis, from Yeddo Sea, exhibited.—Rev. E. O'Meara exhibited some specimens of *Biddulphia Chinensis*, Grev., collected by Mr. Moseley, H.M.S. "Challenger," from the surface of the Yeddow Sea, near Yokohama. This in all essential points agreed with Greville's figure of the examples gathered in the harbour of Hong-Kong, but in some minor details a difference was noticeable. In the figure referred to the surface of the valve seen in front view is represented as hollowed in the middle, whereas in the specimens exhibited the boundary line is generally straight, and in some cases showed a slight elevation in the middle. Moreover, the processes are more robust and longer than they are represented in Greville's figure of the species.

New Closterium from New Jersey.—Mr. Archer showed examples of a Closterium found amongst some Desmidian forms in an old gathering lying in the Herbarium of Trinity College, Dublin, and made at New Jersey, America, kindly given to Mr. Archer by Professor E. Perceval Wright. On the slide, at first glance seemingly a poor one, there were to be detected no less than forty-three species. The Closterium in question is a very robust form, considerably curved and very strongly striated; the striæ very few. It most approached *Closterium costatum*, common in this country. Singularly enough, a single example from New Jersey of that species was opportunely on the slide, quite agreeing with the British and the Irish form, of which he likewise showed a Scotch specimen; and Mr. Archer took the opportunity to contrast it with the new species. This has more of the size and a good deal of the curvature, without the median inflation of *Closterium moniliferum;* its striæ are much coarser than those of *Closterium costatum*. Very opportunely, too, there occurred a Zygospore of the new species on the slide; it is large, suborbicular, thick-walled, and smooth, seemingly not remaining at all attached to the empty parent-cells. This species Mr. Archer would designate as *Cl. crassestriatum*.

Section of Spine of Temnopleurus toreumaticus, exhibited.—Mr. Mackintosh exhibited a cross-section of the spine of *Temnopleurus toreumaticus*, Klein, which showed a single cycle of solid wedges of an irregular triangle-shape, intercalated between which were narrow spokes of reticulated tissue running out from the central pith.

Elongate Unicellular alga, allied to the so-called Closterium obtusum, Bréb.——Mr. Archer drew attention to a unicellular form seemingly, so to say, congeneric with the so-called *Closterium obtusum* (Bréb.), and with those other allied forms Mr. Archer has shown from time to time at the Club meetings, and to which possibly should be added one or two usually, but doubtfully, referred to Spirotænia (including *Spirotænia obscura*). They are all elongate, like Closterium, it is true, with pale clear spaces at the ends, but no moving granules, nor do the green contents form longitudinal radiating laminæ. The present form was but very slightly arcuate, convex on one—the "upper"—margin, straight, or nearly so, on the other—the "lower"—margin, ends slightly tapered and bluntly rounded, the endochrome forming lines running towards the ends. It was thus by its tapering, not cylindrical, figure, and sides not parallel, as well as by its smaller size, distinct from Brébisson's plant. It more resembled in form that shown at the November meeting in 1875, but it was considerably smaller, and the contents wanted the knob-like ending at either extremity, as well as the still single granule suspended in the middle of the cavity. The cell-wall showed here and there certain obvious thickenings, sometimes imparting a certain amount of waviness to the outline. Cell-division transverse, the two young cells remaining appended end to end for some time. Whether the group of forms in question should be relegated to the Desmidieæ at all, and if so, as a distinct and new genus, any more than Ankistrodesmus, for instance, would seem to amount to a begging of the question, inasmuch as conjugation has not been observed in any one of them, if, indeed, the brown so-called Cylindrocystis occurring in the pools on the flat moor above Lough Bray should not be really placed therewith, and which has a smooth orbicular Zygospore.

Winter state of Bryopsis plumosa.—Dr. E. Perceval Wright exhibited some living specimens and a long series of preparations illustrative of a very peculiar mode of growth he had met with during the winter months in *Bryopsis plumosa*. In some cases the long and very tortuous and irregularly knobbed cells were the much altered pinnæ of the frond, which had fallen off and then vegetated in this manner; in other cases these were outgrowths of the base of the frond. In several instances these winter growths assumed the appearance of having oogonia, as in Vaucheria, but in no one instance was a true reproduction seen, and after months of careful watching the specimens were destroyed by an unknown parasitic algal form. It

might be convenient to indicate these winter growths of Bryopsis as its Vaucheria-condition, the history of which has yet to be written.

May 16*th*, 1878.

Section of Ram's Penis, shown under a 1/12 inch Smith and Beck's objective. Mr. B. Wills Richardson exhibited a carmine stained cross-section of a ram's penis he had prepared a few previously. The portions corresponding to the human corpora cavernosa were mostly composed of dense fibrous intersecting bands, the intersections being closest at the part where the septum in the penis of man is situated. These bands passed outwards to join longitudinal bands, also of great density, which formed the outer wall of the section. An artery and a vein, the representatives of the corpora cavernosa vessels in man, passed through the centre of each half of the section. In spaces between some of the decussating bands, near the circumference of the section, there were portions of unstained tissue largely composed of remarkably fine fibres. Clusters of fat cells were seen in some of the spaces. There was no corpus spongiosum, strictly so-called. In the section exhibited it was represented by unstained bands which, as it were, held the urethral wall in position. These were probably cross-sections of blood channels. The urethra itself resembled the collapsed human urethra, being in the section a transverse slit having short fissures leading from it.

Sections of Strongylocentrotus nudus, exhibited.—Mr. Mackintosh exhibited a cross-section of the spine of *Strongylocentrotus nudus*, A. Agass., which showed a small central axis of reticular tissue, numerous well-marked cycles of solid wedges, the whole structure recalling that of *Str. armiger*, A. Agass. described in Club Minutes of April, 1875. The sections being made purposely rather thick, showed the brilliant purple and yellow colouration to great advantage.

New Coscinodiscus.—Rev. E. O'Meara exhibited an undescribed form of *Coscinodiscus* found in material collected by Mr. Moseley in the harbour of Hong-Kong. This form was of considerable size, being ·0143″ in diameter; the middle of the valve perfectly smooth, having a somewhat stellate appearance in consequence of the radiate lines of areoles being of unequal length, the ends of some approaching nearer than others to the centre. The lines of areoles are close, the areoles small throughout, distinctly larger towards the margin. This striking form Mr. O'Meara proposed to name *Coscinodiscus Sinensis* from the locality in which it was found.

Copal with embedded organism, exhibited.—Mr. M'Donnell, lately from Lakes Nyassa and Nyanza, showed a large series of polished pieces of copal, having embedded a variety of insects, leaves of plants, &c., in good preservation, and ready to be submitted to a low power of the microscope.

June 19th, 1878.

Gephyria Dyeriana, exhibited.—Rev. E. O'Meara exhibited a specimen of *Gephyria Dyeriana*, a new species found by him in a gathering made by Mr. Moseley at Kerguelen's Land, and described by him (Mr. O'Meara) in 'Linn. Journ. Botany,' vol. xv, p. 59, pl. i, fig. 10.

Rastelia lacerata, exhibited.—Mr. Pim showed the fungus *Rastelia lacerata* found by him much diffused over a hawthorn-hedge at Woodenbridge, Co. Wicklow.

Cosmarium, n. s., very minute, with finely spinous Zygospore, exhibited.—Mr. Archer showed examples of an extremely minute and rather common little Cosmarium (to give an idea of its size, scarcely so large as the well-known *C. tinctum*), of which, however, the zygospore was not before exhibited or recorded. This little Cosmarium was characterised by a flatness of the top—a small character on which to build a species, some might say—but Mr. Archer thought one could hardly miss to know the species for all that; but further, it is the only one of the extremely minute forms with a spinous zygospore. The zygospore is globular and beset with extremely minute fine and pointed spines, lending thereto an almost hirsute appearance. This was the third occasion on which Mr. Archer had taken this form conjugated. He would call it *Cosmarium lasiosparum*.

Tetraspores in Polysiphonia.—Dr. E. Perceval Wright exhibited mounted specimens, showing the different stages in the evolution of the Tetraspores in *Polysiphonia formosa*. Their point of origin would seem to be always between the central cell and its surrounding cells (siphons). At the base of the central cell a small portion of protoplasm is detached, this then soon divides transversely, the lowermost morsel forms a very minute table, while the uppermost assumes an oval form; this latter remains attached to the former by means of a little stalk of protoplasm, which eventually supports the cell which originates the tetraspores. These are formed by the division of the protoplasm of the cell formed out of the upper oval-shaped mass. It divides into four nearly equal portions; these have no points of attachment to each other. But in the process of growth these four masses gradually arrange themselves after the very characteristic method of these vegetative cells.

July 20th, 1878.

Cylindrocystis crassa and *Mesotaenium violascens* in company from Co. Kerry, were shown by Dr. Moore. These algæ are widely diffused, yet scanty, and it is hard to get a good and pure unmixed gathering.

Chytridium with bacillar zoospores.—Mr. Archer showed a Chytridium on *Eremosphæra viridis* with zoospores caught during egress. The point of interest was their very elongate or cylindrical figure, not, as seems usual, orbicular, or nearly so. With

the bright speck at one end, they had thus a great and curious resemblance to some Bacterian forms.

Cosmarium fontigenum, Nordst.—Mr. Archer showed examples of the only Cosmorium he could find in the stuff labelled *Cosmarium fontigenum* in Nordstedt's and Wittrock's "Algæ exsiccatæ"—this, if it be the form had in view by Nordstedt, is a very common one in this country and in Scotland, but it hardly agrees with the figure accompanying the material. That under view is somewhat like *Cosmarium bioculatum*, but differs in its truncate top, and in possessing a slight depression just beneath the obscure upper angles, thus causing the ends to appear as if somewhat produced. If *this* be Nordstedt's *C. fontigenum*, it would be the first time that author would have so far exaggerated the characteristics of any of the many species brought forward by him as to render the least doubt of the identity, for they are always most truthful and charmingly accurate in all details. It is possible, however, the true form may have yet to be encountered.

Triceratium problematic, shown.—Rev. E. O'Meara exhibited a form of Triceratium found by him in Mr. Moseley's collection at Kerguelan's Land, but only one example of which was met with, and that not quite perfect. It was very large, and the areolation distinct; he could not as yet identify it with any form of this genus as yet described.

Pithophora Kewensis, State of, exhibited.—Dr. E. Perceval Wright exhibited a series of mounted specimens of *Pithophora Kewensis*, and some living specimens, for which he was indebted to the goodness of Sir Joseph Hooker, C.B. This species, described by Dr. Wittrock from specimens found in the Tropical Aquarium at Kew, was in general appearance somewhat like a Cladophora. But it was remarkable to find in the specimens exhibited, which seemed to represent the winter stage of the plant, almost the same branchless, tortuous, and irregularly knobbed filaments as he had shown at the May meeting in *Plumosa*. The resemblance was, of course, only a very general one, for in the one plant we had an unicellular, in the other a multi-cellular algal form; still this stage of Pithophora was well worthy of being very attentively studied.

in my first paper, viz. 5 p. c. solution of chromate of ammonia for twenty-four hours, then washing in water, staining in picrocarmine, and mounting in glycerin.

The hardening reagents that yield good results are chromic acid ¼—½ per cent., especially the above mixture of chromic acid and spirit, and to a certain degree also methylated spirit. Bichromate of potash and Müller's fluid, chloride of gold, and even osmic acid, are not so good; the cell-substance has a tendency to swell up too much. But also when using the first-named reagents it is necessary that the tissue should be fresh. I have found that the lapse of only a few hours between death and hardening is capable of spoiling the appearance to a considerable extent.

When epithelial cells of villi of small intestine of dog, cat, or pig are examined in the perfectly fresh condition in serum, the fibrillar nature, especially the longitudinal fibrils of the cell-substance, comes out very distinctly, although the cell-substance appears as if *uniformly granular;* careful focussing dissolves this into its true nature, viz., being the expression of fibrils seen in optical section. But when the epithelial cells begin to undergo disintegrating changes, such as constantly happen some little time after death, or after the application of pressure, or—what is always the easiest and best means—after the addition of distilled water, the fibrillar nature is lost, the network becoming broken up into irregular unequal fragments; and now the cell-substance presents the appearance as if irregularly and coarsely granular. I have repeated these observations so often with the same result that I am inclined to think that when the substance of the epithelial cells of villi appears uniformly "granular," these granules are the optical sections of the fibrils of the *intracellular network*, but when this substance appears to contain irregular, *i.e.* unequal granules, this is most probably due to a disintegration of the intracellular network, or to the presence of fat-granules.

The nucleus of these epithelial cells is oval, and possess within its membrane a distinct network of fibrils similar to that described in nuclei in my first paper. There is no nucleolus present, but we see small bright dots in the nodes of the network, amongst which we recognise occasionally one or two somewhat larger than the rest. In my first paper I have stated that the majority of the bright dots in the network of the nuclei of cells in the newt are due merely to optical sections of the fibrils of that network, and that the larger particles are local thickenings of the fibrils, either natural or artificial, *i.e.* owing to the shrivelling up of them. This same interpretation I have to apply also to the nuclei of the intestinal epithelium of mammals. As I mentioned in my first paper, Heitzmann describes in various

cells the nucleus as containing a nucleolus, from which fibrils pass in a radial direction outwards into the surrounding cell-substance, where they form a network. That the small regular dots present in the intranuclear network are merely optical sections of fibrils, as also maintained by Eimer,[1] I have not the least doubt of, although Balfour, in his paper on the structure and development of vertebrate ovary,[2] does not accept this interpretation for the bright dots in the reticulum of the germinal vesicle. Looking at some of his figures, *e.g.* figs. 3, 16, 18, I recognise the very identical appearances, *i.e.* uniform dots in the nodes of the network, and I should think a high power, very good light and careful focussing would show that my interpretation is the correct one. That the larger particles occasionally to be noticed in the network are the remains of the substance out of which the network is developed, as Balfour maintains in the case of the germinal vesicle, I have no doubt is the true explanation also of the natural local accumulations which were noticed by me in some nuclei of the cells of newt, and which may be seen also in some of those of the intestinal epithelium. So that we both agree with Schwalbe,[3] who, as I have mentioned in my first paper, regards the nucleolus and other large particles in the nucleus as of transitory value in the developmental history of this organ.

From my own experience I am led to conclude that in the development of the cell-nucleus a stage is reached—in some probably sooner than in others—in which the intranuclear network may be regarded as fully formed, being uniformly constituted and without containing any more of those large particles. Such nuclei may be met with in large numbers in the epithelial cells of stomach of newt, in the endothelial and unstriped muscle cells of mesentery of newt, and also in the epithelial cells of intestine of mammals. In all these organs most nuclei contain a uniform reticulum without any large particles. The small uniform dots present in them, I repeat, are only optical sections of fibrils.

I should invite my friend Mr. Balfour to consider the following simple proposition: the intranuclear as well as the intracellular network having, of course, three dimensions, includes fibrils that lie in the two dimensions of the plan of the field of the microscope, as well as fibrils *placed vertically to it*. The former appear, of course, as fibrils; but, I should like to ask, as what do the latter appear, *i. e.* those situated vertically? Clearly as dots, because they are seen endwise; and for obvious reasons most of them lie in the nodes of the network.

The above stage of ripeness, if I may be allowed to call it so,

[1] 'Archiv. f mikroskop. Anatomie,' Band. xiv, p. 103.
[2] This Journal, vol. xviii (New Ser.), October, 1878, p. 437.
[3] "Bemerk. über d. Kenn. d. Ganglienzellen," 'Jenaisch. Zeitschr.,' Band x, p. 25.

i.e. the uniform network with uniform bright dots in its nodes, belongs to the adult condition of the nucleus. But this is not necessarily limited to cells of the adult, for the nucleus of a cell in the embryo passes just as much through a whole developmental cycle as that of a cell in the adult. Cells of the adult, as well as of the embryo, become mother-cells, and their nucleus, as is now well known, undergoes a series of remarkable changes, the last stage of which, *i.e.* that of ripeness, is the above condition of a uniform network.

In conformity with this we find in the earliest, as well as latest stages of the embryonal life, vast numbers of nuclei, which contain just as uniform a network as the nuclei of small cells of the adult; besides these, there are others in which this network is not so well developed. The same may be said of the nuclei in the cells of the adult. In this respect I quite agree with what Balfour says in his paper of the history of the reticulum in the ova, although I am under the impression that the nuclei of the primitive ova, as depicted in fig. 1 of Plate XVII of his paper, of which he says that they contain a uniformly granular matter, may in reality already include a network, the fibrils of which are very short. I shall have occasion later on to refer to the nuclei of the epithelium of seminal tubes of mammals as containing a dense network of very short fibrils or rods; the appearances presented here are in many respects similar to those of the nuclei of the primitive ova in the above-named fig. 1 in Balfour's paper, but in the case of the nuclei of the seminal epithelium I am able to trace the reticulum very distinctly.

I shall have several times occasion to return to the question of the nucleolus in the different epithelial and gland-cells which I shall have to describe in this paper, and I will limit myself to say here with regard to the nucleus of the epithelial cells of the intestine, that in many instances there is no trace of a nucleolus, and that in some instances there are one or two larger particles contained in the reticulum, the significance of which I have explained above.

The intranuclear and intracellular network are in connection with each other, just as I described it in the case of the epithelial cells of the stomach of newt.

In some nuclei there exists a special arrangement of the intranuclear network in the presence of a layer of circular fibrils situated next the membrane, and arranged parallel to the surface of the nucleus. These fibrils being occasionally viewed perpendicularly are seen as a row of dots next the membrane of the nucleus. A similar arrangement had been noticed also by Eimer,[1] who describes in some nuclei of cells of Salamandra,

[1] Loc. cit., p. 109.

Aegineta, Carmarina hastata, a peripheral "zone of granules" (Körnchenkreis), due to the above circular fibrils. In the case of the nuclei of the epithelial cells of intestine and other organs of mammals this arrangement is not of a general character, as it is absent in many instances. I have seen it only rarely in the nuclei of the cells of stomach and mesentery of newt. But whenever the nucleus contains next its membrane a regular row of granules, it may be taken as certain that this is an index for the circular fibrils. I am inclined to think the same of the row of dots in the germinal vesicle of the ovum, represented by Balfour in fig. 21 on Pl. XVIII, although Balfour does not notice anything of a network in this germinal vesicle.

As is well known, the epithelial cells covering the villi of small intestine and the mucous membrane of large intestine, as well as those lining the crypts of Lieberkühn, possess at their free border a fine longitudinal striation, which, as had been first proved by Brettauer and Steinach,[1] is due to its being composed of minute rods. Thanhoffer[2] maintains for the duodenal epithelial cells of frog that the above fine striation is the expression of contractile processes of the protaplasm of the cells, which processes are said to play an important part in the absorption of fat. Fortunatow[3], however, while opposing this view of Thanhoffer's, mentions the presence of short protoplasmic processes as cilia in the above epithelial cells of frog.

In the case of the ciliated epithelial cells of the foregut of newt, I have mentioned in my first paper that the cilia are distinct prolongations of the fibrils of the intracellular network, and in this respect I was at one with Eberth, Marchi, Eimer, and Nussbaum. The same relation I notice also to exist with regard to the striated border of the intestinal epithelial cells, viz. that the striation is due to *fine fibrils projecting a short distance beyond the general intracellular network* (fig. 1). I cannot definitely decide whether the bright thick cuticle, which apparently lies on the free surface of the epithelial cells, and which apparently contains these fine striæ, is really a cuticle *covering* the cells—as is represented by most histologists since that bright cuticle was first observed by Henle—or is, on the contrary, only a substance arranged *around the free border of the cells* without covering the latter, *i.e.* is a projection of the interepithelial substance, as maintained by Thanhoffer with Lenhossék.

I know of one fact which seems to me to show in a clear manner that the fine striæ, *i.e.* the fine fibrils projecting from the

[1] 'Sitzungsber. d. Kais. Akadem. d. Wiss.,' 1857.

[2] Pflüger's 'Archiv,' viii, p. 391, and 'Centralblatt f. med. Wiss.,' 1876, No. 23, p. 401.

[3] Pflüger's 'Archiv,' Bd. xiv, p. 285.

free surface of the epithelial cells covering the villi, are independent of the above bright cuticle or border substance. I have, namely, seen in sections of villi of small intestine, and also in sections of large intestine of pig—the intestine had been hardened in the mixture of chromic acid and spirit—groups of epithelial cells in which the projecting fibrils could be very beautifully seen *without any bright border substance being present*. There were other groups of epithelial cells in which the other arrangement prevailed, viz. the striæ seen more or less dimly apparently in the bright border substance. Arguing from this fact, one might say that if those projecting fibrils can be present without that bright border substance, they cannot be contained *in* it, for if so the absence of one must necessitate the absence also of the other.

But before definitely accepting this, we have to see whether this same appearance can be observed also in the intestine of other animals, especially carnivorous animals, where this bright border-substance is present to a very considerable extent. And I have indeed noticed on villi of small intestine of dog and cat that in some parts the epithelial cells show beautiful fibrils projecting beyond the free border without there being present any bright border substance.

(*b*) *Of Lieberkühn's crypts.*—The epithelial cells lining the crypts of Lieberkühn are identical with those of the surface of the mucous membrane, both as regards the structure of the cell substance and that of the nucleus (see fig. 2, Pl. VII). All I said above about the arrangement of the intracellular and intranuclear network applies also to the epithelium, and it is therefore unnecessary again to repeat it.[1] True, there are certain differences, but these refer merely to the shape and size of the cell and its nucleus. Thus, comparing the epithelium lining Lieberkühn's crypts of the small intestine with that covering the villi—of course in the same animal—it will be found that the epithelial cells of the latter are conspicuously longer, *i.e.* more columnar than those of the former, and that the nucleus of the epithelial cells of the villi is more regularly elliptical than that of the epithelial cells lining the crypts of Lieberkühn in the same parts, the nucleus in many cells of the latter being circular. Again, comparing the epithelium lining

[1] F. E. Schulze, in his work on epithelial and goblet cells, to be referred to several times in the following pages, maintains that the epithelial cells of the crypts of Lieberkühn differ from those covering the villi, inasmuch as the free border of the former is open, whereas that of the latter is closed by the thick bright border substance mentioned above. This distinction cannot be, however, admitted, because there is in both instances the same bright border substance and the same striation of it, and consequently the explanation of the nature of these appearances must be the same in both kinds of epithelial cells.

the crypts of Lieberkühn of the small intestine with those of the large intestine—of course in the same animal—it will be found as a rule that the epithelial cells are longer in the latter than in the former locality. Besides these permanent differences in size of the epithelial cells of the crypts, there are others that are only temporary, being dependent on the state of distension of the crypt. Thus we notice in the large intestine in some places a considerable difference in the size of adjoining crypts, and also in the length of the epithelial cells lining them. For example, I find in an horizontal[1] section through large intestine of pig as the mean of several measurements :—

a. Diameter of crypt . . . . 0·067 mm. to 0·048 mm.
b. Diameter of lumen . . . . 0·021 mm. to 0·013 mm.

In *a* the length of the epithelial cells is about 0·022 mm.; in *b* it is about 0·015 mm.; the greatest length of the epithelial cells in general is here 0·027 mm.; the smallest 0·01 mm.

Now, the longest epithelial cells are not always found in the largest nor the shortest cells in the smallest crypts, nor do we find the length of the lining epithelial cells the same throughout one and the same crypt. Thus, for instance, I find in a good many places the length of the epithelial cells in the middle part only half or two thirds of those lining the mouth and the fundus of the same crypt. Passingly I may mention that in the short epithelial cells the nucleus is always spherical.

As a rule it may be taken as correct that, *cæteris paribus*, the length of the epithelial cells varies according to the state of distension of the crypt, or according to the amount of mucous secretion present in the cavity of the crypt. Thus I measure in some crypts, distended by mucous secretion, a lumen of 0·054 mm., the whole transverse diameter being only 0·071 mm.; that is to say, the length of the lining epithelial cells is only 0·011 mm. In another place I find a crypt with a lumen of only 0·01 mm. in diameter, whereas the whole transverse diameter amounts to 0·067 mm.; this gives 0·027 mm. as the length of the epithelial cells. Such examples I could multiply *ad libitum*.

It seems to me probable that also the state of contraction of the mucosa, *i. e.* the tissue surrounding the crypts, has something to do with the length of the epithelial cells lining them; the contracted state of the crypts, if I may be allowed to use such a term to indicate those tubes that have a thick epithelial lining and a small lumen, seems to point in that direction. Whether the epithelial cells themselves have the power to actively

[1] The above measurements refer only to horizontal sections and to such crypts, which, by their circular outline, may be regarded cut exactly transversely.

contract and expand, and thereby to change the relation between the thickness of the whole epithelial lining and the size of the lumen, as Engelmann found it to be the case in the small glands of the nictatory membrane of frog, I am not in a position to affirm or to deny. But there seems to be one fact that might be taken as pointing towards a similar relation as that in Engelmann's case, viz. the fact that there are a good many crypts in which, without any formed matter being found in the lumen, this latter (lumen) is more or less distended, and the lining epithelial cells proportionately shortened. This, however, admits also of another explanation, which will appear later on in connection with the submaxillary and other glands. The longer the epithelial cells the more distinct do they show the longitudinal arrangement of the fibrils of the intercellular network.

This change of the shape of the epithelial cells under different conditions is a subject which does not seem to me to have received sufficient attention yet. I shall have occasion in another paper to describe in detail my observations with regard to this subject, but I wish only here to mention a few facts necessary for the interpretation of the above appearances. I have shown[1] that the endothelium covering the pulmonary pleura changes its shape during the respiratory movements of the lung, inasmuch as the individual endothelial plates become flattened during the maximum of inspiration, and return again to their previous shape during expiration. Küttner[2] has shown that with the first inspiration the epithelial cells lining the alveoli of the lung change from columnar cells into flat cells, and this shape they retain in the post-fœtal lung. But I have convinced myself that also in the adult during respiration some epithelial cells of the air-vesicles and also of the bronchi undergo a change of shape. As is known since Elenz and others, the lining of the alveoli of most mammals—especially cat—contain amongst the ordinary flat epithelial cells small cubical cells arranged singly or in groups. F. E. Schultze[3] has very carefully described and figured these appearances.

I find that those air-vesicles of lung of cat that are in a state of expansion, such as is the case in a deep inspiration, possess very few of these small epithelial cells amongst the ordinary flat ones, their number being considerably greater if the air-vesicles are contracted, such as is the case in a deep expiration. These small cubical cells appear to be more "granular" than the other large flat cells, which are more or less hyaline. I am,

[1] 'Anatomy of the Lymphatic System,' ii, Part 1, "The Lungs," p. 2.
[2] Virchow's 'Archiv,' Band lxvi, p. 12, *et passim*.
[3] Stricker's 'Handbook of Histology,' chapter "The Lung."

therefore, led to conclude that these small cubical cells are capable of expansion and contraction. In the first instance they are transparent, large and flat cells, in the second they are less transparent, more granular, smaller and more cubical. During deep inspiration the increase of volume of the air vesicles necessitates an increase of surface of the lining epithelium, and this takes place partly at the expense of those small cells, whereas during a deep expiration the reduction in surface produces again a reduction of some of the large flat cells into small cubical elements. Thus we have precisely the same condition as that in the endothelium of the surface of the pulmonary pleura. But I find also a similar relation to exist with regard to the epithelium of the smallest bronchi.

If in a section of lung I compare a minute bronchus, which—judging by the thinness of its muscular coat and by the large size of its lumen—is to be regarded as being in a distended condition, with one that—judging from the opposite appearances, viz. thickness of muscular coat and smallness of lumen—is in a contracted state, I notice a distinct change in the thickness of the epithelium. In the one case the epithelium is composed of a single layer of short columnar cells; in the other the cells are very elongated, and even so placed as to resemble laminated cells. A similar difference has been pointed out by Arnold[1] with regard to the epithelium covering the mucous membrane of the tongue of frog, viz. that the epithelium is composed of a single layer of cells (grooves between papillæ), but appears laminated where the cells are more pushed together (papillæ themselves).

With reference to the bronchi, I am quite aware that it may be urged that except by comparing two bronchi *of exactly the same order* no definite conclusion can be arrived at as regards the relative thickness of the different parts; and I do not say that in arriving at the above conclusion I have made absolute measurements. But it must be admitted that even without such it is perfectly possible to say in a given preparation whether two bronchi are approximately belonging to the same order, and which of them is contracted and which not. I presume any one who has some experience in the examination of microscopic sections will be capable of determining approximately whether, *e.g.* two arteries seen in transverse section, but of which one is contracted the other distended, are approximately of the same order.

From all I have seen it seems probable that passing from the maximum of a deep inspiration to that of a deep expiration the epithelial cells lining a minute bronchus change from the elongated shape into that of a short columnar cell.

[1] Virchow's 'Archiv,' Band lxiv, p. 203, and passim.

In all these cases of change of shape of the epithelial cells we have probably to do with a definite function which is of importance to the epithelium. If these epithelial cells were not provided with this high amount of contractility and elasticity it is very likely that serious mechanical injury might be inflicted on the epithelium as a whole, if this should be called upon suddenly to cover a surface greatly larger than at a preceding moment.

One of the best illustrations of this kind is the epithelium of the urinary bladder. In a vertical section made through the mucous membrane of a bladder hardened in the expanded condition we notice that the epithelium is considerably thinner than if the bladder had been allowed first to shrink. In the latter instance the epithelium consists of many more laminæ than in the former. [Of course I am not referring to the distortion that takes place if the bladder is extended artificially beyond a certain degree.] To the change in shape of the epithelial cells of the laminated epithelium of the skin and mucous membranes I shall have to return later on.

The *goblet cells* which are found amongst the epithelial cells of the surface, and amongst those of the crypts of Lieberkühn, show, just like those in the stomach of newt, *the intracellular network*; its meshes are wider than in the ordinary epithelial cells on account of the presence of mucin,[1] which, as I mentioned in my first paper, is contained in the meshes of the network. In hæmatoxylin specimens the contents of the goblet cell is stained in a deep purple-blue colour, and on account of this it is by no means an easy matter to distinguish the network; but if the specimen be only slightly stained with hæmatoxylin, or still better, if the sections are stained with picrocarmine, the network comes out with sufficient distinctness. Thin sections of intestine of pig, dog, or cat (hardened in mixture of chromic acid and spirit), are those in which *the network of fibrils in the goblet cells* can be made out distinctly. Fig. 3 represents such a goblet cell, in *a* as viewed from the surface, in *b* from the side. Although the nucleus of the cell had been pressed downwards as far as possible, while the interfibrillar or interstitial substance had swollen up to the extent as to change the shape of the ordinary columnar cell into that of the goblet,[2] it is still possible to discern that there is a connection between

[1] That the goblet-cells contain mucin, which is poured out by them, has been known to Brücke, and has been carefully worked out, besides other things, by F. E. Schulze, in 'Archiv f. mikrosk. Anatomie,' Band 3.

[2] The knowledge that the goblet cells are derived from ordinary columnar epithelial cells we owe to the researches of Brücke, Stricker, and especially to F. E. Schulze.

the fibrils of the intracellular network and the nucleus, although of the network of this latter, for obvious reasons, little can be made out.

From these facts it appears to me that the discussion whether goblet cells are still to be regarded as living cells, or only as degenerated forms of them, loses much of its ground, for the goblet cell is possessed of precisely the same structural attributes as the ordinary columnar epithelial cell from which it is derived, viz. intracellular network of fibrils, nucleus, and a connection between the two. The goblet cell differs from the ordinary epithelial cell only in so far as the interfibrillar or interstitial substance—which is very scarce in the latter—has changed into hygroscopic mucin (or mucigen), and thereby has swollen up to an extreme degree, in consequence of which the network has become much more opened, and the shape of the ordinary epithelial cell has changed into the characteristic goblet. Granted goblet cells are present already during life, if they were due to a degeneration of the ordinary epithelial cells it would be necessary to assume that they have to be got rid of by the mucosa, and that the non-degenerated epithelium had to make up for the defect thus created.

Now, it would be impossible to accept this last assumption if we bear in mind that in some intestines the number of goblet cells is far greater than that of the ordinary epithelial cells.

If part of jejunum of a half-grown dog be examined three to four hours after partaking of food, the epithelium will be found to abound in goblet cells, both that of the surface as well as that of Lieberkühn's crypts. In sections hardened with spirit[1] this will be seen verified. But comparing with this the jejunum of a dog of about the same age that had not been fed for ten to twelve hours, it will be found that the number of goblet cells is greatly smaller. This very well agrees with the assertions of F. E. Schulze, that the goblet cell is a particular stage in the mucous secretion of the ordinary columnar epithelial cell. I have sections through the jejunum (hardened in spirit) of cat, in which both the epithelium lining the crypts of Lieberkühn and those covering the villi contain many goblet cells. Those at the top of the villi possess still their mucin—marked by the deep purple-blue staining—those at the sides and base of villi and of the crypts have got rid of it, their contents being quite unstained ;[2] and it is in these

[1] Since Lipsky it is well known that chromic acid hardening increases the number of goblet cells, but spirit has no such tendency.

[2] I am, however, not quite certain whether this condition does not correspond rather to a state, when the meshes of the intracellular network contain mucigen—that does not stain in hæmatoxylin; so that this state would *precede* the one, when the contents of that network is mucin, *i. e.* does stain in hæmatoxylin.

that the fine intracellular network can be made out with a good power like Zeiss' F, or Hartnack's immersion No. 10.

The intermediary forms between ordinary epithelial cells and goblet cells that one meets amongst the epithelium of intestine trachea, &c., appear to me to be just as likely indicating the return of goblet cells to ordinary epithelial cells as they are generally assumed to be the reverse.

2. *The Ciliated Epithelial Cells of Epididymis.*

Since O. Becker,[1] it is known that the epithelium of the epididymis is composed of ciliated columnar cells. They are always described as consisting of granular protoplasm, and containing an oblong nucleus and nucleolus. Examining sections through the epididymis, hardened in spirit, of half or full grown dog, it will be seen that the substance of the epithelial cells is not "granular protoplasm," but is very distinctly longitudinally striated, being composed of minute fibrils, arranged chiefly parallel to the long axis. Under a higher power these fibrils can be traced through what seems to be the thickened free border of the cell, and projecting as the well-known excessively long cilia. In thin sections through hardened epididymis of dog, the lymphatics of which organ had been previously injected by "puncture" with a 2 per cent. watery solution of Brücke's Berlin blue, I have no difficulty whatever to trace the connection between the fibrils of the cell-substance and the cilia, even only with a moderately high power, such as Zeiss' D or E, or Crouch's $\frac{1}{2}$.[2]

The fibrils constituting the principal part of the cell-substance are, however, connected by short lateral branches into a network, and the "granules" that may be seen along and between them are like those in the intestinal and other epithelial cells, mentioned previously, due to optical sections of fibrils (see fig. 10 of Plate VII).

The nucleus is elliptical, and contains a distinct network with the usual bright dots in the nodes. The network is either uniform, like that found in the nuclei of epithelial and endothelial cells of newt, described in the first part of this paper, or there is next the membrane a special layer of circular fibrils connected by radial branchlets with the more central parts. The bright dots are either of uniform size, and situated in the nodes, being optical sections of fibrils, or there is one or two larger particles—nucleoli—found in the network. The nuclei of the latter kind—*i. e.* with large particles—are in some places fewer

[1] Moleschott's 'Unters.,' ii, 1856.

[2] This lens is certainly a very excellent glass; its definition is as good as any Hartnack's 7—to which it corresponds in magnifying power—that I have examined.

than in others. The fibrils of the intracellular network are also here directly connected with the intranuclear ones; hence the membrane of the nucleus appears dotted, owing to its being interrupted by the passage of those fibrils.

The layer of columnar epithelial cells hitherto described forms one—now doubt the chief—part of the wall of a tube of the epididymis, but there is another layer of small cells with nuclei, generally shrunk and deeply stained in logwood specimens, inside the membrane (Becker, Henle, Kölliker). This latter contains a perceptible amount of unstriped muscle fibres (Henle, Kölliker). See fig. 9, Plate VII.

The nuclei belonging to the columnar cells lie, as usual, in the outer third of the cell-body; in sections, however, hardened simply in spirit, it appears as if the nuclei had a more irregular position, appearing in some cells in the inner, in others near the middle, and in still others in the outer part. Instead of finding the nuclei all arranged in a definite zone—speaking of the epithelium as a whole—we see that they appear distributed almost over the whole thickness of it (see fig. 9, *a*), except a small inner zone that remains free of them. This becomes easily explained if we compare with it a section through epididymis (of the same animal) in which before being placed in spirit the lymphatics had been injected; that is to say, the intertubular spaces having been filled first, the organ was prevented from shrinking. In a section of such an epididymis we find the nuclei approximately keeping within a definite zone of the epithelium.

Out of several measurements of tubes of an epididymis hardened simply in spirit I find:

The thickness of epithelium	0·037 mm.
The thickness of membrane (incl. muscle-fibres) .	0·0055 mm.

For those of the epididymis of the other side, having been first injected and then hardened in spirit, I find:

The thickness of epithelium	0·026 mm.
The thickness of membrane (incl. muscle-fibres) .	0·008 mm.

That is to say, the thickness of the epithelium of the former relates to that of the latter as 3 to 2. The epithelial cells in the former case being more pushed together than in the latter give the impression as if laminated, in the same manner as mentioned by Arnold for the epithelium of the papillæ of tongue of frog, referred to on a previous page.

3. *The Gland-cells in the Submaxillary Gland.*

(*a*) *In the dog.*—As is known from the investigations of Heidenhain[1] the gland cells of the submaxillary gland of dog are

[1] R. Heidenhain, 'Studien des physiol. Institutes zu Breslau,' 1868.

—at any rate in the quiescent state—"mucous cells," *i. e.* glassy transparent cells containing mucus. Lavdowsky,[1] whose work on the anatomy and physiology of the salivary glands is distinguished by a great number of important observations, fully establishes this in showing that in carnivorous animals both the orbital and submaxillary glands are purely mucous glands. The submaxillary gland of man, however, differs in so far from that of the dog that it is a compound gland, including mucous and true salivary gland (Boll, Lavdowsky), and not merely a mucous gland, as stated by Henle.[2]

The cells lining the lumen of the gland tubes (so-called alveoli) are in the submaxillary gland of dog, as is well known, the central or mucous cells of Heidenhain, and outside these we find the "crescents" of Gianuzni, of which Heidenhain has demonstrated that they consist of a group of granular or protoplasmic cells. As regards the former, viz. the central or mucous cells, Heidenhain[3] mentions that their substance is delicately striated. Ewald[4] also mentions a delicate striation of the mucous cells, "as though a perfectly transparent substance was traversed by numerous extremely fine fibrils," and Lavdowsky states that the cells in the quiescent gland contain, besides mucus, traces of protoplasm in the shape of an exceedingly delicate network next the nucleus which, as is well known, lies in that stage more or less compressed close to the wall of the gland-tube.

Heidenhain[5] has asserted that during prolonged secretion the mucous-cells are destroyed, and replaced by new cells formed out of the "crescents," which new cells at first are "albuminous cells" (Asp.) *i.e.* consist of granular protoplasm like the cells of the "crescents," but which are determined to become again transformed into "mucous-cells." In this he is supported by Boll,[6] who mentions the same for the submaxillary gland, especially of guinea pig.

The condition of exhaustion is, according to Heidenhain and Boll, characterised by the replacing of the transparent large mucous cells with parietal compressed nucleus, by "granular" smaller cells with a spherical nucleus placed more or less centrally. That the gland cells possess a different aspect in the two conditions has been confirmed by Ewald, Pflüger and others; but Heidenhain's explanation of this fact has been contradicted

[1] 'Archiv f. mikr. Anatom.,' Band xiii, p. 287.
[2] 'Systematische Anatomie, Eingeweidelehre,' 1862, p. 133.
[3] 'Ber. d. K. Sächs. Ges. d. Wiss.' Leipzig, 1865.
[4] 'Beiträge z. Histol. und Physiol., d. Speicheld d. Hundes,' Berlin, 1870; mentioned also by Pflüger in his article on "Salivary Glands," in Stricker's 'Handbook.'
[5] L. c., pp. 17 and 28.
[6] 'Archiv f. Mikr. Anatom.,' Band v, p. 334.

by v. Ebner, Ranvier and Ewald. Ewald[1] has tried to show what, however, is also hinted at by v. Ebner,[2] viz. that the different aspect presented by the gland cells in the quiescent and exhausted state of the gland is not due to a destruction of the one and a new production of the other kind of cells, but to a direct change of one into the other, the "mucous cells" being convertible by abstraction of mucous into the "granular cells." Lavdowsky,[3] who criticises Ewald's work with what seems to me unjustifiable severity, contradicts Ewald in many things but on several occasions in his (Lavdowsky's) paper he makes assertions which appear to me not irreconcilable with the principal proposition of Ewald, and in a tolerably distinct opposition to Heidenhain's statement. Lavdowsky, on p. 338, writes thus: "We have seen that in the transformation of the mucous-cells there are two processes going on side by side, viz. the diminution of mucous and the appearance of the albuminous substance. Further on it becomes still more distinct that this substance (*i.e.* albuminous substance) *grows more and more* (the italics are Lavdowsky's), while the mucous at the same time *gradually diminishes* . . . . . The reason for this is, according to Lavdowsky, "*the increase* (*growth*) *of one part* (albuminous or protoplasmic), of *the cell substance in order to make up for the disappearance of the other part* (mucous)," and on p. 329 he says that as stimulation proceeds the substance of mucous cells loses the character of mucous, becomes opaque, granular and smaller. This seems to be clear enough; why Lavdowsky should then endeavour to neutralise this again and to put such stress on the destruction of mucous cells and the new formation of protoplasmic cells in the second and third of his stages of stimulation I cannot well conceive. The facts such as delineated in his figures 10, 11, and 12, are perfectly compatible with the first view, viz. "gradual change of the mucous-cells into albuminous cells." That the destruction of mucous cells mentioned by Heidenhain and Lavdowky does not possess more than secondary importance under normal conditions is a matter to which I shall have to return when I give the description of my own observations.

If we examine a thin section through the submaxillary gland, hardened in spirit and stained in hæmatoxylin, of a dog that has been killed twenty-four hours after taking food, the gland having been quickly excised and plunged into the alcohol, we find that it possesses a uniform structure; the gland cells resemble in many respects the mucous cells that we find in ordinary mucous

[1] L. c., p. 31.
[2] 'Die acinösen Drüsen der Zunge,' Graz, 1873, p. 34.
[3] L. c., p. 351 and passim.

secreting glands of the same animal, except, perhaps, that the cells in the former are shorter than in the latter. But the cells are mucous cells, as usually described, of the resting gland, *i. e.* transparent cells containing "mucus" (see below). The outer part of each cell is more or less drawn out and imbricated on the membrana propria, and containing in its extremity the somewhat compressed nucleus; that is to say, the cell resembles a goblet cell. The free border of the cell is open; this can only be ascertained in a part of the section that does not exceed the thickness of one cell; in those parts that are two or three layers deep the cells *appear* covered by a membrane of the same thickness and refractive power as the substance that separates the adjoining cells. The reason is obvious, viz. we see, *de facto*, the substance separating the cells of two layers. I must therefore differ in this respect from the assertions generally given to the effect that most cells are closed towards the lumen. The substance of each cell shows two parts: (*a*), an inner half, transparent and finely striated, owing to the *presence of longitudinal fibrils*, which extend to the free border; for this reason the membrane that in thicker parts of the section appears to cover this inner border seems in a certain focus to be uniformly dotted, owing, no doubt, to it being seen either above or below those fibrils; these fibrils anastomose only by few lateral branchlets. (*b*) An outer half which contains *a uniform network of fibrils*; it is, no doubt, this part of which Lavdowsky (see above) says that there are present in it "traces" of protoplasm in the shape of network. There are not only "traces" but *a well-developed network of fibrils*, and I am rather astonished that Lavdowsky has not seen and figured it more clearly, for the appearances are very conspicuous. As in the case of the epithelium of the intestines the nodes of this network appear like dots, and with only a moderately good lens one might easily mistake this part for "granular." The fibrils of the inner part are distinctly connected with the network of the outer part. The distinction into these two parts can be made out when we have a clear profile view of the cells, in an oblique or horizontal view we do not, of course, perceive this distinction. When the cells are viewed as a mosaic, *i. e.* in bird's-eye view, the substance of each polygonal figure appears to be composed of a uniform network, but this probably is only the network of the outer cell portion just mentioned.

The "crescents" of Gianuzzi or "parietal cells" of Heidenhain, appear well developed, and I do not find them in any way different, as regards number and disposition, from what they are described by Heidenhain, Lavdowsky, and others. Their substance is a *dense network of fibrils*. There are lobules or

portions of lobules in which the crescents are conspicuously better developed than in other parts, and on careful comparison it will be found that also the central or mucous cells of these parts appear larger and better stained in hæmatoxylin. The contents of the mucous cells are here of a more or less distinctly purple-blue tint, whereas in the other lobules, the mucous cells are not stained at all or only slightly so. We know from the observations of Dr. Watney[1] that in ordinary mucous glands, *e. g.* in the tongue, we can, with the aid of hæmatoxylin staining, easily ascertain which gland or parts of gland are just in the act of mucous secretion and which not, for where the cells are charged with mucin they stain in a characteristic purple-blue tint. The thicker the layer the more pronounced the colour. Dr. Watney showed me this very characteristic reaction also in the test-tube; even the smallest quantity of mucous —no matter what its reaction, whether alkaline or acid—becomes precipitated by the addition of a drop of hæmatoxylin solution —the usual watery solution of extract of logwood—as flakes of deep purple-blue to blue colour.

Hence it becomes clear that also in the submaxillary gland the blue staining of the mucous cells is due to the presence of mucin in them.

I am quite aware that, as Heidenhain, Pflüger and v. Ebner have pointed out, there is in the submaxillary as well as in other mucous glands a post-mortem change of the "mucigen" into mucin, but this takes place only if the gland be not placed early enough into the hardening spirit. In the above description I was referring only to those cases where immediately after the animal had been killed by bleeding, small bits of the organs had been placed into the spirit. Besides, these glands that have suffered that post-mortem change do not show well the outlines of the cells (v. Ebner), as I can fully confirm. In my case I have another more weighty reason for assuming the presence of mucin in the mucous cells already in the living, it is the fact that in those lobules the ducts contain mucin stained in the purple-blue tint.

From these facts, viz. that there are present lobules or parts of lobules in which the "crescents" are enlarged and the mucous cells are charged with mucin, not "mucigen," as in the resting state, and that also the corresponding duct contains mucin, I infer that in the so-called resting state of the gland, but provided the animal be kept without food for some time, there are parts in which the formation of mucin out of mucigen is already going on. I shall have to mention further below a similar relation in the mucous glands of tongue and œsophagus of the same animal.

Lavdowsky also states[2] that in the resting glands there may

[1] 'Proceedings of the Royal Society,' vol. xxii, p. 293, and 'Philosoph. Transactions,' 1876, ii, p. 772.

[2] L. c., p. 318.

be seen already under a lens small, well-defined, more transparent quasi-gelatinous portions, which under the microscope show the characters, not of resting gland, but of one that has slightly secreted, and he also notices the enlargement of the "crescents" or parietal cells. The mucous cells, according to Lavdowsky, show no change in these parts, except that their nucleus is slightly larger and more rounded. I do not find this alteration in the nucleus. Had Lavdowsky used hæmatoxylin staining for these parts, he would not have failed to notice that the mucous cells are altered also in another respect, inasmuch as they contain mucin instead of mucigen, besides being somewhat larger. Carmine staining, which Lavdowsky chiefly used, does not show this difference in the contents of the mucous cells.

In the salivary gland of a dog, killed twenty minutes after partaking of food, most ducts contain mucus, and in most lobules we find the cells filled with mucin.

A comparison of a submaxillary gland, as described above, with one taken from an animal (dog) killed one hour after feeding, shows the following differences:—Although there are a good many parts where a difference between the gland structure taken from this animal and one that had been killed twenty-four hours after the last meal cannot be detected, still there are other parts—sections of lobules, and even whole lobules, in which the mucous cells are decidedly shorter. Their substance appears more uniformly pervaded by the minute intracellular network of fibrils, whereas the parietal cells are somewhat more prominent, being larger. The nucleus of the mucous cells does not present the same appearance or position as in the other case, being less compressed, more irregular, and not so close to the membrana propria.

Pflüger first pointed out[1] that in the intralobular ducts—the part that he called "Speichelröhren"—the columnar epithelial cells lining them are in their outer portion composed of minute longitudinal rods, whereas the inner portion appears more or less homogeneous or slightly granular; the circular or slightly oval nucleus lies about the point where the two parts are in contact.

Like Pflüger, I see that in some tubes the epithelial cells show a very fine striation also in the inner part; and on looking at this with a high power I am able to make out that these longitudinal fibrils form also a network, and hence the "granular" appearance of this part. Unlike the other observers, I notice that the nucleus of these epithelial cells contains a uniform network, generally including only the uniform dots, occasionally though not frequently containing also a large particle, corresponding to the nucleolus of some authors. Further, I notice

[1] 'Archiv f. mikrosk. Anat.,' Band v, p. 193.

in thin sections that *the fibrils of the outer cell portion are in connection with the intranuclear network*, hence the membrane of the nucleus presents the appearance of a perforated membrane. Pflüger[1] and Lavdowsky[2] assert that when a part of this "rod-epithelium" is viewed from the surface we see a uniformly dotted substance; and Heidenhain[3] has also maintained, with reference to the epithelium of the convoluted tubes of the kidney, on the occasion when he first described those cells as being in the principal part composed of rods or fibrils, that in the surface view these cells appear uniformly dotted, owing to the rods being seen endwise. Lavdowsky[4] confirms this for the embryonal kidney. Without, of course, doubting for a single moment that what Heidenhain and also Lavdowsky isolated in the respective kidneys were rods or fibrils, I must differ from both and Pflüger, not only with regard to the cells of the submaxillary gland, but also with regard to those of the convoluted tubes of the kidney, for a careful inspection of the surface of the rod-part of the epithelium in both cases shows, not merely a dotted appearance, *but a network, i.e.* dots with short anastomosing branches, the dots being of course due to rods seen endwise. So that the rod-part of the epithelium does not merely contain a bundle of rods or fibrils, as maintained by Pflüger, Heidenhain, Lavdowsky and others but a *reticular substance* which possesses a pre-eminently longitudinal arrangement. Whether the rods or fibrils are in many instances membranous expansions or not, I am not able to say, although looking at them endwise I seem to notice in some places appearances more compatible with the presence of the latter than the former. The same arrangement is possesssed by the "rods" in the medullary sheath of nerve fibres, described by Lantermann and MacCarthy, that is to say, the medullary sheath is not merely composed of vertical rods, but of a reticular substance. I shall have occasion to refer to this appearance more in detail in the third part of this paper.

In both cases of glands hitherto described there are found a number of alveoli, which possess no "mucous cells," or only traces of them, but which are entirely, or to the greater extent, made up of "granular" or "protoplasmic" cells, with circular central nuclei. I find either small groups or sections of lobules almost entirely made up of such small protoplasmic cells; they are for the most part polygonal, possess one central circular nucleus, they lie very closely together, and appear either to belong to more or less convoluted tubes without any lumen in them, or they are arranged, as in the ordinary alveoli, around a very small lumen,

[1] Stricker's 'Handbook,' English trans., p. 431.
[2] L. c., p. 314.
[3] 'Archiv f. mikrosk. Anat.,' Bd. x, p. 5.
[4] L. c., p. 333.

and resemble then in all respects the alveoli of true salivary glands, or the so-called *serous glands* known through A. Heidenhain and von Ebner (see further below). They are always in connection with a tube given off by one of the salivary ducts with rod-epithelium (*i. e.* Pflüger's "Speichelröhren") and lined with short pavement epithelium. In some parts it is also seen that in the above alveoli with "granular" epithelium, one or two of the cells are already *mucous cells*, but the whole alveolus is much smaller than an ordinary one. There can be little doubt that in the submaxillary gland of half-grown dogs (I worked with animals six to eight months old) there exists a certain amount of unripe gland-structure, but in different stages of development, consisting of intermediary forms between more or less solid chain-like masses, composed of polygonal uninuclear "granular"[1] cells, then groups of such cells around a small lumen, and finally such forms in which some of the "granular" cells are replaced by "mucous cells."

Pflüger mentions that in the resting submaxillary glands of rabbits there are "thousands" of young cells, developing in connection with the rod-epithelium of the salivary ducts. Lavdowsky denies this, and says that Pflüger probably mistook the aggregate of cells constituting the "crescents" for developing cells. Although I have not been able to see in the resting submaxillary gland of dog anything like the cells that Pflüger delineates,[2] I must oppose Lavdowsky's statement as regards the non-existence of developing cells in any but stimulated glands. As I have pointed out above, there is a perceptible amount of gland tissue, in the half-grown dog, just passing through the different stages of development.

The above intermediary forms between alveoli in which some of the "granular" cells have changed into mucous cells and alveoli entirely composed of "granular" cells distinctly shows us the relation that exists between the mucous cells and the "granular" cells of the crescents. This relation coincides entirely with that stated by Heidenhain and Lavdowsky for the exhausted gland, viz. that the parietal cells, or the cells of the crescents give origin to the mucous cells. That this is the relation in the growing parts of the gland, of this I have no manner of doubt, but I have likewise no doubt that *while the submaxillary gland is in a normal state of function*, such as is represented in the ordinary life of the animal, *the "mucous cells," as a whole, are not destroyed during secretion*, and that, therefore, there is no need for their being regenerated from the parietal cells. I must

[1] I use the word "granular" as indicating the appearance of the substance of the parietal cells, but of course I have stated above that these granules are only apparent, that substance being in reality a dense network of fibrils.

[2] Stricker's 'Handbook,' fig. 93—95.

place myself on the side of those (Ewald, v. Ebner, Ranvier) whose observations of this and similar glands, especially mucous glands, has led them to the conclusion that "mucous cells" possess in the different phases of function a different aspect, that they are not destroyed during secretion, but after secretion are capable of returning again to the former state of rest. Such is the conclusion to which a general consideration of secretory action would, *à priori*, lead us, and the above observations fully bear that out. They have shown us that mucous cells possess a state of rest, in which they show an inner more longitudinally fibrillated and an outer more reticulated part, containing in its meshes the "mucigen." Then there is another phase, that of secretion, in which the cells are larger, and the "mucigen," transformed into mucin; after this the cells again return to their former state, first, however, showing a more uniform network of fibrils. The nuclei of the mucous cells are subjected to only one change, viz. in the last phase they are less compressed, approaching more or less the spherical shape.

But although I do not admit that under normal conditions of function Heidenhain's theory is applicable, I do not say that such is not the case under certain abnormal conditions. The observations of Heidenhain, Boll and Lavdowsky leave no doubt that if the gland is exhausted by a long-continued stimulation, the alveoli assume a uniformity of structure, all the cells appearing of the nature of the "granular" cells of the crescents. Heidenhain explains this, as stated above, by saying that all the mucous cells having been destroyed the parietal cells have to make up for them. Lavdowsky,[1] on the other hand, shows that this is partly due to the mucous cells changing into small "granular" elements, and partly to a new formation of such cells from those of the crescents. That the alveoli in a young condition contain only "granular" cells, some of which change into mucous cells, this I have mentioned above, and from this experience I am not at all disinclined to accept the explanation of these authors, if it can be shown that the mucous cells are destroyed in great masses. As far as my experience goes of glands in normal function, I have not seen any mucous cells changing into cells that at all look like the parietal cells, and for this reason I cannot accept the force of the argument of Ewald, who by a process of "mucous abstraction" tries to render the mucous cells similar in appearance to the parietal cells. Ewald's experiments do not seem to me to prove at all that Heidenhain's explanation is not correct, for Ewald does not tell us that he ever saw in any phase of the secretion the mucous cells actually *turn into* "granular" cells similar to those of the crescents.

[1] L. c., p. 329.

I said above that the condition of "exhaustion" (Heidenhain and Lavdowsky) of the submaxillary gland of dog is an abnormal one, inasmuch as in the ordinary process of function no such condition is ever observed as that described and figured by these observers. To produce that condition Lavdowsky had to stimulate electrically the secretory nerve (the chorda in the case of the submaxillary gland, the n. buccinatorius in the case of the orbital gland) from three to seven hours and more, a proceeding which has no parallel in the normal function of these glands.

(δ) *In man.*—I possess a good many preparations of submaxillary glands of children that died in the course of scarlatina. The glands were obtained very shortly after death, and, after having been hardened in spirit, were found in an excellent condition. As I described in my paper on the "Anatomy of Scarlatina,"[1] the interlobular tissue contains accumulations of lymph cells, a sign of interstitial inflammation; but besides this, in some of the glands the gland structure, both of alveoli and ducts, appears normal, the gland-cells in their mutual relation and distinctness of outline being perfect. I shall refer in the following to these glands only.

α. In sections through the submaxillary gland of a child aged 7, we find—amongst the great mass of lobules the alveoli of which are lined with more or less distinctly columnar "granular" cells with a round nucleus in the outer part, *i. e.* true salivary cells—a few lobules much larger than the others, in which the alveoli are lined with mucous cells, *i. e.* columnar transparent cells, the nucleus of each cell being more or less compressed and situated in the outermost part of the cell. The alveoli lined with mucous cells are larger than the others, owing to the lumen and the cells being larger. The relatively great amount of connective tissue separating the lobules enables us to trace the outlines of the individual lobules with far greater facility than in the dog.

β. In a gland of a child aged 8, I found, on the other hand, only traces of mucous gland structure, these being reduced to a few groups of a very limited number of alveoli lined with mucous cells, interspersed amongst the bulk of lobules composed of salivary gland tissue. The cells of the latter are columnar "granular" cells, with a round nucleus in the outer third, and are arranged around a small lumen.

γ. In a gland of a child aged 12, I find no trace of any alveoli lined with mucous cells; the lobules are all uniformly made up of alveoli lined with beautiful columnar cells of "granular" protoplasm.

If we now examine more carefully in the first case the

[1] 'Reports (No. viii) of the Medical Officer of the Privy Council,' 1876, p. 79.

lobules containing mucous gland structure, we ascertain with unmistakable clearness that the alveoli lined only with mucous cells *are directly continuous* with alveoli lined for a greater or smaller section with granular cells, the rest being mucous cells, and, further, with alveoli, which are altogether lined only with granular cells. Those alveoli that are only partly lined with granular cells resemble in many instances the alveoli of dog's submaxillary gland, viz. the central cells being mucous cells, whereas the granular cells form the crescents. That alveoli of this kind are directly continuous with such that are lined exclusively with granular cells, of this I have convinced myself quite positively.[1] It is hardly necessary to add that the last-named alveoli are smaller than the others.

I have been able to confirm this observation made on Case *α*, also in Case *β*. In both instances I find in those alveoli that are lined with mixed epithelium the mucous cells possess a nucleus less compressed and not so close to the membrana propria as in the alveoli that are lined only with mucous cells.

That the intermediary forms, previously stated, are not due merely to different stages of development of mucous gland-structure, as in the submaxillary gland of half-grown dog, but probably to different states of function, is shown in Cases *β* and *γ*, which, *although belonging to older individuals, show less of the mucous gland-structure* than in Case *α*.

We are, then, led to the conclusion that there exists an intimate relation between the gland-structure lined only with "granular" cells and such with only mucous-cells. Boll, in the above-named work, stated that in the submaxillary gland of guinea-pig the alveoli are either lined by mucous cells or by protoplasmic "granular" cells, and he concluded that whole lobules are capable of being transformed into mucous-secreting structures. The submaxillary gland of dog is, according to the same author, the one extreme; that of the guinea-pig, in which all alveoli are lined by "granular" cells, is the other extreme; that of man is intermediary between the two.

Lavdowsky denies this, and maintains that the two structures, —viz. alveoli lined with mucous cells and such lined with "granular" cells—are entirely independent of each other, and are only co-existing side by side, as is the case in the submaxillary gland of man, or, as is still more evident, in the root of tongue, where we find side by side both varieties of gland-structure, viz. serous glands and mucous glands (v. Ebner).

[1] The examination on this point is greatly facilitated by the distinctness with which we are enabled to trace what belongs to one and the same lobule, owing to the fact—as above mentioned—of the presence of considerable masses of connective tissue between the lobules.

From my experience of human submaxillary gland, above described, I am in agreement with Boll and in opposition to Lavdowsky; but differing from Boll, I assume here not only a change of the alveoli lined with granular cells into such as are lined with mucous cells, but, *vice versâ*, a change of mucous cells into "granular" cells.

Whether in my cases this change is observable in the absolutely normal gland under normal conditions of function, or whether it is found only so in consequence of prolonged secretion—in the cases of scarlatina, from which the above glands were derived, there was a considerable amount of throat affection, and hence most likely a prolonged secretion of all glands leading into the oral cavity—must be determined by further investigations.

In the lobar ducts of the human submaxillary gland we find that the epithelium is composed of a superficial layer of beautiful columnar epithelial cells and a deep layer of small cells, the former possess very elongated nuclei, the nuclei of the latter being oval. The nuclei of both contain a uniform network of fibrils, with the usual bright dots in the nodes, but no large particles comparable to a nucleolus. The columnar cells show a distinct bright striated border like the epithelial cells of intestine, only not so broad, and I have ascertained that also in the ducts of the submaxillary gland the bright border has nothing to do with the striation, the former being sometimes absent, and the latter can then be made out as being due to the ends of longitudinal fibrils, of which the cell-substance appears chiefly to be made up. But we find also here on close inspection that these fibrils form a network.

The lobular ducts possess the same rod-epithelium as in the submaxillary gland of dog.

4. *The Epithelial Cells of Mucous Glands.*

The gland-tubes (Puky Akos[1]) of mucous glands are usually described as possessing a relatively large lumen, lined by more or less granular cells, whose nucleus is in some glands round, and situated in the outer part of the cell, in others it is very indistinct, being much compressed and close to the membrana propria.

Heidenhain, on the occasion of his investigations of the submaxillary gland of dog (loc. cit.), pointed out that this gland is in many respects similar to the ordinary mucous-secreting glands of other parts, for he found also in some of these a distinction between parietal "granular" cells and central mucous cells. In the mucous glands of the lip of man and rabbit, in those of the

[1] 'Sitzungsb. d. k. Akad. d. Wiss.,' Band. 60, ii, 1869.

larynx of dog and rabbit, this author found besides alveoli containing mucous and "granular" cells also such that are lined with only "granular" cells.

V. Ebner[1] investigated the mucous glands of the tongue of man and the various domestic animals, and he found that the alveoli are lined with glassy columnar cells of a granular contents, which is mucous; the nucleus is generally indistinct, but after reagents is seen as a small roundish or elliptical flattened body next the membrana propria. This author mentions a difference between the mucous glands of the tongue of carnivorous animals, on the one hand, and those of the tongue of rabbit and guinea-pig on the other, consisting in the presence of crescents in the former; in the latter they are absent. But v. Ebner adds, that these crescents are not comparable to the groups of granular cells in the submaxillary gland of dog, which Heidenhain spoke of as forming the crescents, but that they correspond to thickened (nucleated) parts of the membrana propria, *i. e.* to what Boll (loc. cit.) mentioned as "crescent" in the submaxillary gland.

Tarchetti[2] describes in the mucous glands of the trachea two distinct forms of gland cells; one corresponding to mucous cells, the other to the more opaque protoplasmic parietal cells; the latter in some places completely occupy parts of the alveolus, in others they are reduced to "crescents."

Ladvowsky examined the mucous glands of different regions (oral cavity, larynx and pharynx), and he describes[3] the changes they undergo when their secretory nerves are subjected to stimulation (electrical or chemical). These changes are in all respects similar to those that he found in the submaxillary and orbital glands, subject to the difference that the above mucous glands do not contain any (protoplasmic) parietal cells. The changes are these: the nucleus becomes rounded and enlarged, then the substance of the mucous cells loses its mucous character, "owing to the increase of their protoplasm;" the cells become gradually smaller and granular. In consequence of this alone the alveoli become smaller.

I have examined mucous glands in man and the domestic animals of different parts of the body—tongue, palate, pharynx, œsophagus, larynx and trachea, and I have arrived at the conclusion that, as in the submaxillary gland of dog, the gland cells possess different morphological characters during rest and secretion, which (characters) in some respects correspond to those mentioned by Heidenhain and Lavdowsky of the mucous glands, but in other respects differ from them.

a. In the dog.—If the mucous glands of the tongue or œso-

[1] L. c., p. 19.
[2] 'Rivista di Medicina,' &c., December, 1874.
[3] L. c., p. 335.

phagus be examined in sections of specimens hardened in spirit and stained in logwood, it will be seen that the cells lining the alveoli are beautiful columnar cells having almost the same size in the same alveolus; these vary, however, amongst each other, both as regards the diameter of their lumen and the lining cells, as will be mentioned below. The cells are in all cases open, their free surface not being covered by any membrane. They contain an exquisitely beautiful network of fibrils which uniformly pervades the cell substance, and which can distinctly be perceived with even a D of Zeiss, or $\frac{1}{5}$ of Crouch (see fig. 4, Plate VII). In some alveoli I can distinguish also here an inner more longitudinally striated part from an outer one with a uniform network, but the number of such cells is relatively small, and is to be met with only in alveoli in which no actual secretion is going on (see below). When viewing the cells from the surface, —*i. e.* when viewing the mosaic formed by the ends of the cells —the network is equally distinct. Some of the cells like those in the submaxillary gland possess a process with which they are imbricated on the membrana propria. The nucleus is recognised as a shrunken deeply-stained body pressed against the membrana propria, and situated usually in one of the corners of the cell, that is to say, the cells resemble goblet cells. When viewed from the surface the nucleus appears more or less rounded in shape, and in some instances contains a uniform network.

The membrana propria of the alveoli is very distinct. In our sections it appears as a bright membrane, with staff-shaped nuclei from place to place. The membrane being thicker where a nucleus lies, we obtain the appearance of attenuated "crescents," such as described by Boll in the submaxillary gland, and (as mentioned above) found also by von Ebner in the glands that we are dealing with. Such is invariably the character of the cells and membrana propria, no matter in what state the gland is, viz. whether filled with mucin or not. The following two conditions of the alveoli and tubes of the gland of the tongue may be noticed:

(*a*) The cells lining the alveoli do not contain any mucin, the interfibrillar or interstitial hyaline substance (contained in the intracellular network) remaining unstained in hæmatoxylin, but the network is very distinct. The lumen of the alveoli and ducts is empty. The alveoli differ in size to a considerable extent: from alveoli of 0·04 mm. in diameter, and a lumen of 0·01 mm., to such that measure 0·054 mm. in diameter, and 0·013 m lumen. The length of the cells varies between 0·015 to 0·02 mm. (*b*) The cells are filled with mucin; they stain, therefore, a more or less deep purple-blue tint; so do also the contents of the lumen of the alveoli and ducts, these contain the same sub-

stance, *i. e.* mucin. The cells lining the alveoli are longer; this is the more pronounced the more distinctly they stain in logwood, *i. e.* the more mucin they contain. In some alveoli the lumen is enlarged owing to the presence of a great mass of mucin, and in this instance the diameter of the alveolus as a whole is naturally greater. I see no difference as regards distinctness of the intracellular network, the shape and position of the nucleus, and the distinctness of the membrana propria with its nuclei in the above two states.

Thus, just as in the submaxillary gland of dog, we see also here that under normal conditions two different states are to be distinguished: (*a*) one where the gland cells contain in the meshes of the network a homogeneous substance corresponding, not to mucin, but to mucigen; this is the state of rest; and (*b*) a state of secretion, when the gland cells increase in size owing to the change of mucigenous substance into mucin, but the intracellular network remains otherwise unaltered. Lavdowsky (l. c.) showed us in addition to these two states a third one, which does not, however, occur under ordinary normal conditions, *i. e.* (*c*) a state of exhaustion, when the cells decrease again in size, becoming at the same time more "granular," and their nucleus more spherical. According to my view of the structure of the gland cells this is not due to an increase of the network (protoplasmic part, Lavdowsky), but merely to an exhaustion of the mucigenous, *i. e.* interstitial, substance.

Precisely the same two states that we noticed in the normal gland of the dog are found also in the glands of the œsophagus and larynx and soft palate of the same animal. There are, however, certain differences in structure in these different glands which it is necessary to mention here. They are these: while the alveoli of the mucous glands of the tongue possess minute rudiments of what in shape corresponds to nucleated crescents, but what, as I mentioned in conformity with v. Ebner, are merely nucleated parts of the membrana propria (Boll); the alveoli of the mucous glands of the œsophagus in the dog possess real protoplasmic "crescents," independently of the membrana propria and the mucous cells surrounding the lumen. They are granular, nucleated parietal cells in the sense described by Heidenhain of the submaxillary gland. They are not very numerous, not far so numerous as in the submaxillary gland, but sufficiently distinct to be noticeable. Thus I find in one place a "crescent" that measures 0·038 mm. from one pointed end to the other, and 0·006 mm. in thickness—some crescents are even thicker—and in it five oblong nuclei; but what is of greater importance is that outside this crescent I trace very clearly the membrana propria, and this possesses a staff-shaped nucleus just

where it embraces the "crescent," so that the two structures, viz. membrana propria with staff-shaped (profile view) nucleus, and crescent composed of granular uninuclear cells, are here seen side by side; and we are therefore enabled to say that these mucous glands possess granular parietal cells just like the submaxillary gland. If I compare alveoli whose mucous cells and lumen are filled with mucin, with alveoli that are not in a state of secretion, I do not see any perceptible change in size of the crescents; in the submaxillary gland we saw that their size is increased; but I should not like to pronounce definitely on this point, because the relatively small number of the crescents is not very favorable for determining that. However this may be, there is at any rate no *conspicuous* alteration, for then we should most probably not fail to discern it.

Much greater, however, than in the œsophagus is the number and size of the "crescents," composed of polygonal granular[1] parietal cells, in the glands of the pharynx of young dogs, in which, side by side and *directly continuous* with alveoli containing a fair number of granular parietal cells, there are others that are *entirely* composed of granular cells, polyhedral in shape and possessed of a rounded or oblong nucleus. Alveoli of this kind are smaller than the ordinary alveoli, and possess either only a trace of a lumen or hardly any lumen at all. We have here the same appearances that I mentioned on the occasion of the submaxillary gland of young animals. That also in the case of the pharynx the alveoli composed entirely of granular cells represent a stage of development, and are not alveoli with "exhausted" mucus cells in the sense of Lavdowsky, nor alveoli in which the mucous cells have been destroyed and replaced by the parietal cells, is proved by the following facts:—(*a*) They are present in great numbers in the young animal, and only in the most peripheral parts of the gland-tubes; (*b*) they are connected both with tubes in which the gland cells are in a state of rest, and with such in which these are charged with mucin.

In the epiglottis of the dog the same condition obtains as regards the mucous glands, viz. there are tubes lined with well-developed mucous cells differing in no way from those of other mucous glands; in addition to these we have tubes that contain "crescents" of granular cells; and finally in connection with these we find alveoli which, to a greater extent or almost entirely, consist of "granular" cells.

In the trachea of cat the number of tubes lined only with granular cells arranged round a distinct lumen is very great indeed. The ordinary mucous cells are in this animal fine columnar cells, which differ from those of dog, inasmuch as

[1] I need hardly repeat that their substance is not in reality granular, but, as in the previous instances, a dense network.

their nucleus is not compressed and situated so close to the membrane propria, being a more or less well-shaped spherical body situated in the outer part of the cell near the membrane propria.

(*b*) *In man.*—The mucous glands of man which I had the opportunity of examining are those of the tongue, palate, œsophagus, larynx and trachea. These organs were obtained very shortly after death, and in some instances I have succeeded in obtaining preparations which, as regards the preservation of the elements, are not inferior to those I obtained from animals freshly killed.

In the glands of the tongue and palate we find the same relations as in the glands of dog, both as regards the intimate structure of the mucous cells, and also as regards their different stages of function. The alveoli in the human mucous glands of these organs possess no real "crescents," *i.e.* none composed of "granular" cells. There is, however, a difference between the mucous glands of man and dog, which consists in the fact that in the former, when in the state of rest, the nucleus of the mucous cells is not so compressed and not so much pressed against the membrana propria as in the latter, being more rounded, and as in other columnar epithelial cells, *e.g.* intestine, situated in the outer portion of the cell. But when the cells of the human mucous glands are in a state of secretion, *i.e.* when the cells are larger and filled with mucin, the nucleus resembles in its compressed shape and its peripheral position that of the mucous cells of the dog's gland when in the same state.

The alveoli or gland tubes of the scarce mucous glands of the human œsophagus present themselves in the following states: (*a*) either they are lined with beautiful columnar cells, which on account of the dense nature of the intracellular network, appear "granular," the fibrils having however predominantly a longitudinal arrangement, hence the cell-substance appears more or less distinctly longitudinally striated; each cell possesses a spherical nucleus, situated in the outer part and containing a uniform network. (*b*) Or the alveoli are lined with mucous cells of the ordinary description with a nucleus pressed against the membrana propria; the cell-substance is clear, and its network open like that of ordinary mucous cells; we notice also here that the network has a different arrangement in the inner and outer portion of the cell, in the former being more longitudinally arranged—hence this part appears longitudinally striated,—in the latter the network is more uniform. The interfibrillar or interstitial substance, *i.e.* the substance contained in the network, in some alveoli a clear homogeneous substance—mucigen; in ters it is stained deeply with hæmatoxylin—mucin, the cell

being larger in the latter case. In these alveoli also the lumen contains mucin. (c) Finally there are glands in which some alveoli are lined at the same time with granular and mucous cells side by side.

A similar interesting condition is presented by the mucous glands of the human larynx and trachea, especially of the epiglottis, where the same alveolus, lined both with granular columnar cells and mucous cells side by side, is the common occurrence. (See also Tarchetti mentioned above.)

In fig. 5 I have faithfully represented a part of an alveolus of a mucous gland of epiglottis lined by "granular" cells and mucous cells. It is here also shown that the "granular" cells possess a striated border, and I have to repeat here what I have stated already several times before, viz. that the striæ are due to the fibrils of the cell-substance, and that the bright border-substance is independent of it. If we place side by side the experience thus gained in the examination of the human epiglottis and œsophagus, we are led to the conclusion that in these organs the state in which mucigen and mucin is present in the gland cells is preceded, or followed respectively, by a state in which the cells possess the same character as for instance the epithelial cells of the intestine, viz. in which the interfibrillar or interstitial substance is present only in an infinitesimal amount, and hence the closeness of the network and the granular appearance. This corresponds very probably to the condition observed by Lavdowsky (l. c.) in the exhausted mucous glands.

The ducts of the glands of the human œsophagus are in their deeper section lined with a layer of columnar epithelial cells, and outside this a layer of small polygonal cells; the former show a beautiful longitudinal striation. The same structure is to be observed in the columnar epithelial cells lining the ducts of the glands of the human larynx and trachea.

The occurrence of the columnar "granular" epithelial cells side by side with, and changing into the mucous cells in the glands of the epiglottis of man shows us the identity of this appearance with that observed in the intestine (the surface of the mucosa and in the crypts of Lieberkühn), viz. the presence of ordinary "granular" columnar epithelial cells side by side with mucous secreting goblet cells and the convertibility of the one into the other. That the mucous cells in mucous glands are identical in shape, structure and function with the goblet cells of the intestine has been mentioned previously more than once.

Before concluding this chapter I must say a few words concerning the "serous" glands of the tongue treated in so excellent a manner by v. Ebner in his monograph above quoted. The gland cells lining the alveoli of these glands are not composed of "granular" protoplasm as represented by

v. Ebner, but show a very beautiful and dense network of fibrils; hence their apparent granulation. Preparations of the "papillæ foliatæ" of rabbit's tongue hardened first with Müller's fluid and then with methylated alcohol, as also the parts of human tongue containing the circumvallate papillæ hardened in our mixture of chromic acid and methyl. alcohol above mentioned, yield very good results. All that is necessary is to examine a very thin part of a section, stained with logwood, with a good high power. It will then be also noticed that the nucleus does not contain a "granular" substance nor a nucleolus, but a uniform network with the usual dots in the nodes. The intranuclear fibrils can be traced through the membrane of the nucleus into the intracellular network. At the same time we notice that whereas the cells lining the peripheral alveoli of the lobules in the serous glands of rabbit are polygonal as stated by v. Ebner, they are beautiful columnar cells in the glands of man.

5. *The Cells of the Glands of the Stomach and the Duodenum.*

In this paragraph I wish merely to state my observations as regards the structure of the cells lining the above glands.

(A) *The glands of the fundus.*—As is well known from the researches of Heidenhain,[1] Rollett[2] and others, the cells called by Heidenhain chief cells, by Rollett adelomorphous cells, are distinguished from the parietal cells (Heidenhain), or delomorphous cells (Rollett), not only by their different shape and position, but also by their different aspect, the former being more transparent than the latter, which by their "granulation" are always more conspicuous. Examining the two kinds of cells in the glands of the fundus of man, pig, cat and dog, in the fresh state, or after maceration, or in specimens hardened with chromic acid and spirit, I find that the substance of both the chief cells and parietal cells is composed of a more or less distinct network of fibrils with this difference, that in the latter the network is much denser, hence its "granular" appearance. And also the nuclei of both show a uniform network, especially the nucleus of the parietal cells is, in this respect, of a very regular appearance. The best method to show these minute structures is to harden the above glands, especially of dog, first in a mixture of chromic acid (2 parts of $\frac{1}{2}$ per cent.), and methylated alcohol (1 part), and after four or five days to complete the hardening in methylated spirit. Thin sections stained in hæmatoxylin show

[1] 'Archiv f. Mikrosk. Anat., Band. vi, p. 336.

[2] 'Centralblatt,' 1870, Nos. 21 and 22; and Rollett's 'Untersuchungen,' 2 Heft., 1871.

the network of both the parietal and chief cells very beautifully. The chief cells contain in these specimens a network very similar to that described above of the mucous cells, but the meshes of the network are not quite as large in the former as in the latter. Comparing the chief cells of the fundus of stomach of a dog killed twenty-four hours after partaking of food (the stomach being found empty), with the same cells of a dog, about the same age, one hour after a copious meal of meat, it is seen that in the latter instance they are larger (Heidenhain), and that they show the network *more distinct*, being more open than in the former.

In figure 17 I have represented the appearances presented by the chief cells and parietal cells of fundus of stomach of dog, the stomach having been hardened in the above mixture of chromic acid and spirit. As I mention in the explanation of figure 12 to the plate vii, accompanying this paper, the structural appearances presented by these stomach glands are in many respects similar to those of the mucous glands of pharynx and submaxillary gland of dog. The mucous or central cells of the latter differ from the parietal cells of the "crescents" in the same manner as the chief cells differ from the parietal cells of the stomach, viz., in the nature of the intracellular network.

The epithelial cells lining the duct of the peptic glands are, during digestion, *e.g.* in a dog killed one hour after meal, loaded with mucin.

(B) *The glands of the pylorus.*—Ebstein[1] has shown that the cells lining the gland tubes of the pylorus of stomach of dog possess a different character in the state of hunger and in that of digestion; in the former the cells are of a clear, finely granular contents, their nucleus being flattened and situated next the membrana propria, in the latter the cells are shorter, more opaque, and their nucleus round and situated more towards the centre of the cells. Ebstein has also pointed out that although the cells lining the pylorus-glands contain a certain amount of mucus, they are not mucus-secreting cells like those of the ordinary mucous glands, with which they have generally been compared, but are to be placed in the same category with the chief cells of the glands of the fundus. Bentkowski[2] confirms Ebstein's observations.

I am in a position to confirm these assertions of Ebstein, in so far as I find the cells lining the pyloric glands of dog presenting two different aspects according to the state of the stomach. First, the cells are found to be transparent, slender columnar cells with a cup-shaped nucleus pressed against the membrana propria; the cell substance is a distinct network of fibrils, the meshes containing a clear homogeneous substance.

[1] 'Archiv f. Mikrosk. Anatomie,' Band. vi, p. 528.
[2] 'Medicin. Zeitung,' Nos. 14, 15, 17 and 18, 1876.

Secondly, the cells are considerably shorter, their substance is a close network of fibrils, hence their aspect is more granular than in the former state; their nucleus contains a uniform network is less compressed, but not quite round, and is slightly more removed from the membrana propria than in the former state; this second state is found only after prolonged secretion. In both stages, however, the cell-substance presents more or less a longitudinal striation owing to the network being arranged more or less longitudinally. Unlike Ebstein, I have found in a good many glands during digestion real mucous cells as in the mucous and submaxillary glands, *i.e.*, I have seen the interfibrillar or interstitial substance staining with logwood like mucin does, and for this reason I think that these cells are not quite so removed from mucous secretion as Ebstein states. The columnar epithelial cells lining the ducts of these glands and covering the free surface of the mucosa are, during digestion, loaded with mucin, as has been known to F. E. Schultze, Ebstein and Watney. In the dog I have never seen them otherwise but open, and I agree therefore, with F. E. Schultze and Biedermann against Ebstein, who states that they are closed in the state of hunger, and is therein confirmed, at any rate for the pylorus of rabbit, by Watney (loc. cit., p. 471).[1]

In my article on "Stomach," in Stricker's 'Handbook,' p. 543, I have stated that neither in the human stomach nor in that of dog do I find such a definite boundary between the peptic and the pyloric glands, as had been maintained by Henle, Kölliker, Donders, Leydig and others, but that the unbranched glands containing peptic cells merge into the branched glands of the pylorus lined with simple columnar cells. These latter were then always described as the mucous glands in contradistinction to the peptic glands of the fundus. Rollett (loc. cit.) has contradicted that assertion, inasmuch as he found always a sharp contrast and boundary between the two kinds of glands. Ebstein (loc. cit., p. 517), on the other hand, while agreeing with Rollett that the mucous membrane of the regio pyloria contains *only* glands that are lined with columnar cells, and does not contain any so-called peptic cells—*i.e.*, cells corresponding to the parietal cells of Heidenhain, finds in the stomach of dog a small region, "*intermediary zone*," in which, between the so-called mucous glands, one or two peptic gland tubes may be met with. This zone is, according to Ebstein, about 1—1·5 centim. broad, and lies just where the brownish mucous membrane of the

[1] I agree with Watney that the nuclei are in no stage of digestion so round as represented by Ebstein, at any rate not over very large parts of the stomach, although I think Watney goes too far in saying that they are *always* discoid, *i. e.* congressed; this, although true for specimens prepared with chromic acid, is not applicable to spirit-specimens.

fundus contrast with the pale membrane of the pyloric region. I have examined carefully this intermediary zone of Ebstein and *the parts next to it* in the stomach of dog, and I must more than ever maintain my original assertion, viz. that in these parts the two kinds of glands merge into one another.

When approaching the pyloric region, we find the peptic glands considerably altering their appearance. (*a*) The so-called stomach pits or ducts, lined by the same slender columnar epithelium as the free surface, become considerably longer; while their length in the peptic glands of the fundus in most cases amounts to about 0·1 mm., and only rarely exceeds 0·15 mm., we find them near the regio pyloria as long as 0·28 mm. The longest ducts of the mucous glands of the pyloric region when measured in a section cut exactly vertically do not amount to more than 0·3 to 0·35 mm. So that we have the ducts gradually increasing from a length of about 0·1 mm. in the fundus to 0·28 mm. near the pyloric region, and to 0·3 and 0·35 mm. in the pyloric region itself.

(*b*) In proportion as the ducts increase in length the rest of the gland tube decreases.

(*c*) Whereas in the fundus the peptic gland tubes, except the deepest section which is more or less curved and bent, are little deviating from what can be fairly described as a straight course vertical to the surface, we find them near the pyloric region very greatly bent, and what I must specially accentuate, *often branched* into two or three tubes; this is the case not merely in the deepest portion,—for a branched condition of this is occasionally met with also in the fundus,—but as in the pyloric glands at any point of the gland tube.

(*d*) In looking through specimens made from parts *near* the intermediary zone, we find the greater majority of the gland tubes of the same breadth, including the same small lumen, and presenting the same distinction into chief cells and parietal cells, and also the same distribution of these, as in the gland tubes of the fundus. But we find amongst these several instances where the gland tubes approach those of the pyloric region, *being much broader and containing a much larger lumen, presenting, however, still a distinction into chief cells and parietal cells*, with the difference that these latter are *considerably scarcer* than in the other peptic glands.[1] This change in the size of the tube and its lumen is to be noticed first in the deepest parts of the glands, and I have several instances before me where the breadth of the tube and its lumen are not a shade smaller than in those of the pyloric glands. As is well known, the comparatively

[1] Bentkowski (l. c.) arrived at a similar conclusion in the examination of the stomach of dog and pig.

narrow body and small lumen of the peptic glands of the fundus of dog's stomach form a very marked contrast with the broad tubes and large lumen of the so-called mucous glands of the pylorus of the same animal, and for this reason the above-named change of the tubes in these characters is of importance.

(*e*) In this I do not refer, like Ebstein (l. c.), to the occurrence of "a few peptic gland tubes amongst a series of mucous glands," but to *a few broad tubes with large lumen lined with columnar epithelium and containing only a few parietal cells, amongst a majority of ordinary peptic gland tubes.* These broad tubes resemble the tubes of the pyloric glands in every respect; they are branched, and their columnar epithelium lining the broad lumen in no way differs from that of the above glands; and if it were not for the facts (*a*) that we still find a few parietal cells, and (*b*) that towards the neck they pass into a narrow gland tube with small lumen and a goodly number of parietal cells, we could not distinguish them from the tubes of the mucous glands.

The preparations to which I here refer were hardened in the mixture of chromic acid and spirit mentioned several times; the lumen of the peptic gland is lined with *cells which in all respects resemble those lining the tubes of the pyloric glands, i. e.* transparent columnar cells with the characteristic cup-shaped, *i. e.* compressed nucleus close to the membrana propria. In this I see a fact in support of Ebstein's theory of the identity of the chief cells of the peptic glands with the cells lining the pyloric glands.

I have before me a specimen in which I find the following condition: a very large duct—0·08 mm. broad and 0·28 mm. long—branches into *four* tubes, two of them differ in no way from the other peptic glands present in the vicinity; they are relatively narrow, have a small lumen, are somewhat convoluted, and present the usual number of parietal cells. The other two are exactly like them in the neck and the beginning of the body of the tube, but in the deeper part they differ inasmuch as both are very much broader; one of them (No. 3) is just as broad and its lumen just as large as a gland tube of the pylorus; and the other (No. 4) is somewhere between the ordinary peptic and pyloric gland. And in conformity with this alteration we find also in No. 3 *very few parietal cells*—I count two parietal cells only from the neck to the fundus of the tube. In No. 4 they are more numerous, but considerably fewer than in Nos. 1 and 2.

The breadth of tube No. 1 or 2 does nowhere exceed 0·013 mm., its lumen is hardly measurable with an Ob. 7 of Hartnack; in tube No. 3 the breadth of the tube is 0·07 mm., and the lumen 0·013, *i. e.* the lumen alone is as big in No. 3 as the whole tube in Nos. 1 and 2.

After these facts I am justified in saying that the two kinds of glands, viz. the peptic glands of fundus and the so-called

mucous glands of the authors (single peptic glands of Ebstein) in the pyloric region of dog merge into one another.

(*C.*) *The glands of Brunner.*

I fully agree with those observers who have maintained the great similarity in appearance of the cells lining the glands of Brunner, and those of the pyloric end of the stomach (Schwalbe,[1] Hirt,[2] Watney[3]); and I can likewise confirm the assertion of Cobelli[4] and Watney[5] as to their anatomical continuity, or rather the gradual transition of the pyloric glands into the glands of Brunner in the duodenum. As regards the minute relations of the cells of the latter glands, I should especially refer the reader to Schwalbe's exhaustive paper. Like Hirt, I know two stages of the cells lining these gland tubes (Schlemmer[6]) (*a*) one in which the cells are thin, long, columnar cells, open at their free end; their substance is transparent and containing a network of fibrils with more or less open meshes; the nucleus is cup-shaped and pressed against the membrana propria; and (*b*) another stage, in which the cells appear shorter and thicker, the network of their substance very close, so that this appears very "granular," the nucleus round and near but not quite close to the membrana propria. In both states the cells appear longitudinally striated, but especially so in the latter. In figs. 6 and 7 I have represented these two states, and the difference appears sufficiently clear. But just as in the case of the pyloric glands, so also here the state *b* does not correspond to the state of secretion in the sense named by Ebstein for the pyloric glands, and by Hirt for the Brunner's glands, but rather to a state after prolonged secretion or exhaustion, for during the first hour or two after taking food and in the state of hunger the cells always present the appearances described above sub *a*.

In preparations prepared with spirit, provided the cells present themselves in state *b*, *i.e.* with a spherical nucleus, we find in many nuclei one or two large bright particles—nucleoli—included in the intranuclear network. With a high power I am able to trace that these large particles are not simple structures, but represent a shrunken part of the network.

6. *The Liver Cells.*

As I mentioned in the first part of this paper, Kupffer[7] had

[1] 'Archiv f. mikr. Anatom.,' Band. viii, p. 133.
[2] In a letter by Prof. Heidenhain to the Editor of the 'Archiv f. mikr. Anatom.,' Band. viii, p. 279.
[3] L. c., p. 477.
[4] 'Sitzungsb. d. k. Akad. d. Wiss.,' Band. l, 1867.
[5] L. c.
[6] 'Sitzungsber d. k. Akad. d. Wiss.,' Band. 60, i, 1869.
[7] 'Festschrift,' an Carl Ludwig, 1875.

stated that the substance of the liver cells of frog consists of a hyaline ground substance—paraplasma—and of a granular-fibrillar contractile "protoplasma." With reference to the liver cells of mammalian animals, I can fully confirm that observation, finding that their substance is composed of a minute network, in whose meshes is included a hyaline substance; we have here what we mentioned on so many previous occasions, an *intracellular* network of fibrils, and in this an *interfibrillar* or *intestitial* hyaline substance. As has been noticed by many observers, the substance of the liver cells appears when examined under many different conditions—fresh in saline solution, aqueous humor, or macerated in iodised serum, solution of bichromate of potash or Muller's fluid, especially when hardened in spirit, chromic acid, or Muller's fluid—of a "uniformly granular" character. This "uniformly granular" aspect is due to the very close nature of the intracellular network, as I explained on several previous occasions. In the liver of guinea pigs, the portal vein of which had been injected with a 2 per cent. solution of Brücke's Berlin blue, then hardened in spirit and stained in carmin or hæmatoxylin, I find (*a*) in many acini the liver cells composed of a uniform, beautiful and open network of fibrils and membranes, in connection, through the nuclear membrane, with a similar network pervading the nucleus itself. Next to cells of this kind I find (*b*) such in which the network, although its parts are still distinct, is somewhat closer, and it requires a higher power to distinguish it so clearly as in the former. And lastly, I trace these to (*c*) cells in which the network is so close that its constituent fibrils cannot be made out. The cell substance appears uniformly and densely "granular." The gradual transition from cells of the nature of *a* to those of *b* and *c* leave no doubt that the uniform "granulation" is due, as mentioned before, to the very close condition of the network. In fig. 20 I have represented liver cells in which the intracellular network is seen of the character mentioned, sub. *b*, *i.e.* medium grade of closeness.

The liver cells, in which the meshes of the network are comparatively widely distended, are considerably larger than those whose substance appears densely "granular," and this is easily intelligible, if we remember that the distinctness of the network is due to the distension of its meshes. Whether in the course of functional activity the liver cells show such differences of the network, as we mentioned on several previous occasions (mucous glands, Brunner's glands, intestinal epithelium, &c.), I am not in a position positively to assert, although I have noticed certain facts which lead me to believe that also in the liver-cells a difference of the appearance of their network corresponds to a different state of function. Thus, for instance, I have found

that in a liver—hardened in 80 per cent. of methylated spirit, or in our mixture of chromic acid and methylated spirit,—obtained from a dog killed either after having been kept without food for twenty-four hours or one hour after taking its food, the liver cells show a more open network, *i. e.* the interstitial substance is present in a greater amount, than if the liver be taken of an animal that had been killed five or six hours after partaking of a meal, in which case the cells appear more uniformly "granular," *i. e.* the network closer and the interstitial substance less abundant.

The nucleus of the liver cells is spherical, and contains a uniform network. Some nuclei show a regular layer of peripheral circular fibrils mentioned on a former page. Spirit preparations often reveal in this network one or more central or eccentric large dots—nucleoli; in some livers, hardened in strong spirit, there is hardly a liver cell that does not possess a nucleolus, but in other livers, hardened in 80 per cent of spirit or in chromic acid, I see only few liver cells whose nucleus possesses a nucleolus.

For this reason alone it cannot be regarded as an important element. When examining carefully with a high power (Hartnack, immersion 10) a series of nuclei which contain what would generally pass for a "characteristic, large and bright nucleolus," I find that twice out of three times I can see that it is a complex structure, and traceable to a part of the intranuclear network having shrivelled up. But besides the small bright dots due to optical sections of fibrils, there are undoubtedly larger particles in some intranuclear networks, but these are smaller than the above "characteristic" nucleoli.

In the nuclei of liver cells that show the intracellular network with open meshes, *e. g.* the liver of guinea-pigs injected with 2 per cent of Berlin blue, the intranuclear network does not contain as a rule any traces of larger particles; it is a uniform network and anatomoses with the former by a great many radiating branchlets. I do not agree with Kupfer, according to whom the network is most conspicuous around the nucleus, for in those instances in which I find the network in its greatest distinctness and beauty (see guinea-pig's liver treated as above stated), I see that it pervades the substance of the liver cells in an uniform manner. In some instances of the injected guinea-pig's liver I have seen this network assume a faint blue tint on that part of the cell that is next to a capillary vessel, but I presume this is due to an imbibition of the network with the Berlin blue. In many places *the network of one cell is seen in direct connection with that of the neighbouring cells.*

In conclusion, I wish to mention an appearance which I have

met with in the liver of dog, pig and guinea-pig, hardened in spirit and also in chromic acid; it is this:—The substance of some liver cells presented two more or less distinct zones, one smaller one apparently homogeneous, or faintly granular and stained in hæmatoxylin; and a larger one, more transparent, not stained, and showing the above network more or less distinctly. The nucleus of these liver cells is situated peripherally, generally more or less closely to the homogeneous zone, or even in it. The appearances in this latter instance are to a great extent similar to those presented by the cells lining the gland tubes of the pancreas (Langerhans[1] and Heidenhain.[2]

7. *The Cells of Laminated Epithelium.*

In this paragraph I wish to notice merely the structure of the more or less polyhedral cells forming the middle and deeper strata of the laminated epithelium, *e.g.* oral cavity, pharynx, œsophagus and anterior surface of cornea, and of the rete Malpighii of the epidermis.

With reference to the epithelial cells of the first, I have convinced myself in fresh specimens and in specimens prepared by macerating bits of the above organs in iodized serum, 5 per cent. chromate ammonia—the same method being used as described in my first paper with regard to the examination of stomach of newt—and in sections after hardening with our mixture of chromic acid and spirit, that the substance of these cells, usually described as of more or less uniformly granular appearance, consists of a dense network—*intracellular network* (see fig. 18 A). The nucleus of these cells is likewise permeated by a delicate network with the usual small bright dots in its nodes (see fig. 18 B). There are occasionally seen in it one or two larger particles, comparable to the nucleolus auct., but the number of nuclei containing it is in some parts extremely small. I miss them, for instance, in cells in which, of all others, one would have supposed they should be present, viz. in the deepest cells of the laminated epithelium, for it is these cells which, according to the observations of most writers, are concerned in the process of reproducing the epithelial cells of the layers above them. Thus, in preparations of the deepest epithelial cells of the cornea I do not find, in the majority of instances, any signs of distinct nucleoli, and the same must be said also of the deepest cells of the epithelium of the œsophagus, pharynx and tongue. Nay, even in the regeneration of epithelium of cornea after a superficial defect, of

[1] 'Beitr. z. mikrosk. Anat. d. Bauchsp.,' Inaugural Dissert, Berlin, 1869.

[2] 'Pflüger's Archiv,' Band. x, 559.

which organ I made specimens either in chloride of gold, or spirit, or in chromic acid, I miss a nucleolus in the majority of epithelial cells. These contain a uniform network of fibrils. And I will take this opportunity of saying that the statements by Mayzel[1] and Eberth,[2] to the effect that during the regeneration of epithelium those nuclei that contain filaments, or a network of them, are peculiar forms of developing nuclei, is in so far erroneous, as every nucleus contains such a network. But it is quite possible that under those special conditions the intranuclear network becomes more prominent and distinct, and therefore more easily visible, although I do not notice in my specimens any marked difference in this respect.

The cells of the middle layers of the epithelium of the human œsophagus, obtained soon after death, show the intracellular network and fibrils passing from one cell to the other. If a section through this epithelium be examined with the new excellent $\frac{1}{12}$ inch oil-immersion of Zeiss, the intranuclear network, the connection of this with the intracellular one, and the passage of bundles of fibrils from one cell to the other, is as distinct as one can wish.

In the flattened cells of the superficial layers of the epithelium of the first passages of the alimentary canal, I cannot trace the intracellular network with distinctness, but the nucleus, except in the most superficial cells, still contains the network. The nuclei of even the most superficial cells of the epithelium of cornea of frog, newt, or mammalian animal, when examined fresh or in sections after hardening in chloride of gold and then spirit, or spirit alone, or chromic acid, show the intranuclear network with more or less distinctness.

I have seen the intranuclear network in several instances even in the squamous cells spontaneously detached from the epithelium of mouth and floating in saliva.

The same structure, *i. e.* intracellular and intranuclear network, is also possessed by the epithelial cells of the deeper and middle stratum of the rete Malpighii of epidermis. The "prickles" between these cells, first observed by Max Schultze[3] in the cells of the middle layer of the epidermis and laminated epithelium of oral cavity, are directly connected with the intracellular network, and form at the same time the connecting fibrils between adjacent cells (see fig. 19). This is quite in conformity with the observations of Bizzozero[4] and Heitzmann[5]. This last-named author

[1] 'Centralblatt,' No. 50, 1875.
[2] 'Virchow's Archiv,' Band 67.
[3] 'Centralblatt,' 1869.
[4] 'Studi f. n. Laboratorio patol. d. Univ. d. Pavia,' 1870.
[5] 'Untersuch. über d. Protoplasma,' 'Sitzungsber. d. Akad. d. Wiss.,' Band, lxvii, 1873; ii, p. 14 of 'Separatabdruck.'

maintains that every epithelial cell, no matter whether in the rete Malpighii, or the laminated epithelium of a mucous membrane, or in gland tubes, is a "prickle-cell," *i. e.* connected with its neighbour by fine processes, and that every nucleus of these cells is possessed of processes—that is to say, is a "prickle-nucleus" (Stachelkern), and the nucleolus of each of these "prickle-nuclei" is similarly constituted, *i. e.* is a "prickle-nucleolus" (Stachelkernkörperchen). In the foregoing pages I have several times mentioned the relation and value of what is generally described as a nucleolus to the rest of the nucleus, and we have seen that its nature is in many instances a very doubtful one, and its occurrence variable and inconstant, and I cannot therefore accept what Heitzmann says of this pseudo-organ. Nor can I agree to the proposition that *all epithelial cells*, no matter where they are found, are "prickle-cells."

There is one other point which I have to mention in connection with the cells of the laminated epithelium of those parts which are capable of being placed in folds, *e. g.* skin, œsophagus and pharynx. It is this, that the shape of the cells of the deeper and middle strata may be entirely altered by the different condition of contraction of the subjacent membrane. If, for instance, a small piece of the above organs, while being hardened in spirit or chromic acid, is left altogether to itself, it will shrink into folds to a considerable degree. In vertical sections through these structures the rete Malpighii, or the laminated epithelium respectively, is found to present a different aspect on and between the folds, inasmuch as in the former instance the epithelial cells of both the middle and deeper strata possess an elongated shape, their long axis being parallel to the vertical diameter; in the parts between the folds the epithelial cells, on the contrary, are more elongated in the horizontal direction, *i. e.* are more flattened. But if during the hardening those membranes are prevented from an excessive shrinking by fixing them on cork or bone or cartilage, the shape of the cells of the above-named layer will be found of the typical character which is generally ascribed to them, viz. the deepest cells more or less columnar, the following ones more or less polyhedral, gradually becoming flattened as the surface is approached. And for this reason the rete Malpighii of the epidermis of the ear-lobe, for instance, appears different from that of ordinary skin that had been allowed to shrink during hardening; in the former, where the skin is prevented from shrinking by being fixed on the cartilage, the rete Malpighii is of the typical appearance; in the latter the cells of the middle and deeper stratum of the folds are very much elongated in a vertical direction.

In connection with this change of shape we also see that the

intracellular network has a somewhat different arrangement; in the elongated cells it also assumes an elongated arrangement parallel to the long axis of the cell, so that the cell-substance appears longitudinally striated.

This appearance belongs to the same kind as the one I described in the first chapter, viz. the alteration of shape and arrangement of epithelial cells, owing to a change of the membrane on which the epithelium is situated.

8. *The Epithelial Cells of the Testis.*

In this paragraph I wish to describe chiefly the structure of the nuclei of the epithelial cells of the seminal tubules and of the so-called parenchymatous cells between them (tubules).

(*a*) If we examine a section through testis of full grown cat, dog or guinea-pig, hardened in our mixture of chromic acid and methylated spirit, or in pure methylated spirit, we see that the nuclei of the polygonal, or more or less rounded cells which in several layers line the seminal tubules, possess a great many minute rods connected into a network. At first sight the nucleus appears coarsely and uniformly granular, but on careful inspection we ascertain that these coarse granules are the sectional view of shorter or longer rods. The network formed by them possesses on this account a somewhat different appearance from that mentioned on several preceding occasions, and I refer the reader to figure 15, A and B, of Plate VII, where I have represented these appearances. The nuclei of all except some of the most external cells, *i.e.* those next the membrana propria, are spherical and possess the network of the short rods mentioned just now. The nuclei of the last-named cells are, however, oval, and contain the more uniform network of fibrils mentioned of other nuclei.

The same character of a network of short rods may be observed in the nuclei of the multinuclear large cells present in some of the seminal tubes of cat and dog (v. La Valette). There is nowhere any sign of a nucleolus.

The intranuclear network comes out with great distinctness in preparations of testis treated with a 5 per cent. solution of chromate of ammonia, and subsequent staining in picro-carmine in the manner described in my first paper of stomach of newt.[1] I should especially recommend for class-demonstration of a beautiful intranuclear network to use the testicle of full-grown newt, and to prepare it after the method with 5 per cent. solution of chromate of ammonia and subsequent staining in picro-carmine.

[1] L. c., p. 319.

There are several interesting appearances connected with the spermatozoa of newt's testis *prepared in this manner* which I shall have occasion to describe at a future time, but one I wish to mention already here on account of its very great distinctness and also on account of the great facility with which the preparations may be obtained and preserved. If after staining the testis in picro-carmine a small particle of its interior, after having been teased out with needles, is mounted in a drop of glycerine, we notice an innumerable mass of isolated spermatozoa, *each of which possesses a fine but distinct spiral filament coiled round the whole element*—head, middle section and tail; the spiral thread begins near the anterior pointed extremity, is most distinct round the middle section and tail, and terminates at a short distance from the end of this latter; it is not distinct on the thick part of the head.

(*b*) The connective tissue between the seminal tubes of the testis contains peculiar epithelial-like cells, which have been known to all who have investigated the testis. They have been generally described (v. Ebner, Hofmeister, and others) as connective-tissue cells of the interstitial tissue. Waldeyer[1] regards them as a peculiar kind of connective-tissue cells which he calls plasma-cells. Mihalkovic,[2] who accepts Waldeyer's interpretation, has described them very fully in the testis of the various domestic animals. Harvey[3] regards them as belonging to the nervous system, *i.e.* as ganglion cells.

As is well known, they occur in considerable numbers—chiefly as forming anastomosing tracts—in the testis of cat, dog, and especially guinea-pig. Their shape is generally that of a polyhedral cell, being more or less uniformly pressed against one another; their nucleus is spherical. The substance of these cells is not a "granular" protoplasm, as usually described, but an exquisite network of fibrils. In sections of testis of cat or dog (hardened in our mixture of chromic acid and spirit), stained in logwood, this network appears with great distinctness, its meshes being relatively open. In figure 14 A I have represented very faithfully this appearance. The intracellular network is, however, much denser in the cells of testis prepared with 5 per cent. solution of chromate of ammonia and subsequently stained in picrocarmine; it is represented of guinea pig's testis in fig. 14 B.

The nucleus of these cells contains in all instances the ordinary network of fibrils in connection with the intracellular network In the case of the testis hardened in chromic acid and spirit, the nucleus of most of the cells in question contains one or even two central or excentric larger particles included in the network. In specimens prepared with chromate of ammonia most of the nuclei contain an uniform network without any large particles. The intracellular network is very beautifully shown in the pecu-

[1] 'Archiv f. Pathol. Anatom.,' 1872.

[2] 'Berichte d. Math. Phys. Klasse d. Königl. Sächsischen Gesellsch. d. Wiss.,' July, 1873.

[3] Harvey, R. T., 'Centralblatt f. d. Med. Wiss.,' 1875, No. 30, p. 498.

liar polyhedral epithelial-like cells that form similar tracts in the matrix of the ovary. Both kinds of cells, viz. those of testis and ovary, are placed by all observers in the same category on account of their similarity of appearance and their development. I notice, however, that in these epithelial-like cells in sections of hardened ovary of kitten, cat and guinea pig, in which animals they occur in considerable quantities, the intracellular network is considerably denser than in the cells of the testis. These cells, —both of the testis and ovary of young and adult animals—are in respect of their morphological characters[1] in no way different from epithelial cells, and as regards their development it has been satisfactorily shown that, with reference to the ovary, they are remnants of the epithelium of the Wolffian body (His, Waldeyer, Romiti, and others). Balfour, who describes this same tissue very minutely in the *developing* ovary of rabbit, dog, cat and sheep,[2] as "tubuliferous tissue," also connects it with the Wolffian body. The same holds good also for the interstitial cells of the testis of the *adult*, viz. they are *remnants of the epithelium of the Wolffian body that has not been used for the development of the epithelium of the seminal tubes.* Hence, we may justly call them *interstitial epithelial cells* of the testis and ovary.

9. *The Epithelial Cells of Sebaceous and Sweat Glands.*

(*a*) The intracellular network of the cells forming the epithelium of sebaceous glands—I only refer to the flask-shaped or tubular secreting parts, not to the ducts—is in many respects analogous to that mentioned in the liver cells. If we examine the peripheral parts of a sebaceous gland in sections of skin (of man, but especially of sheep), hardened either in chromic acid, or our mixture of chromic acid and spirit, and stained with logwood, or carmine or picro-carmine, we notice that the substance of the small polyhedral cells lining the membrana propria is not 'granular,' but consists of a very dense and uniform network, and there is, therefore, hardly any interfibrillar substance perceptible. The cells next these peripheral ones are larger, and the network is more distinct and open, and the nearer to the centre of the tube the larger are the cells, and the more open is the network (see fig. 16). The interfibrillar substance which is here the fatty matter constituting the sebum, increases therefore as the cells approach the centre, and thus the network becomes more open.[3] This network is visible only after the removal of

[1] Neither Kölliker ('Gewebelehre,' 1867, p. 524), nor Henle (Splanchnologie,' p. 358), gives a correct description of these cells.

[2] L. c., p. 422.

[3] The reticular nature of the substance of these cells has been demonstrated to me by my friend Mr. McCarthy several years ago.

the fatty interfibrillar substance, on account of the high refractive index of this latter. (In preparations mounted in dammar varnish or Canada balsam solution, this is effected by passing the sections first through alcohol and then through oil of cloves.)

All these cells possess a nucleus containing a uniform network.

Towards the duct the nucleus of the cells becomes indistinct and the intracellular network is reduced to a few membranous streaks, between which the fatty matter is enclosed. Thus the epithelial cells lining the alveoli of sebaceous glands are in all respects analogous to the other secreting cells, especially mucus-secreting cells; in mucus-secreting cells we had mucin as the result of the change of the interfibrillar substance; in the epithelial cells of sebaceous glands we find it to be a fatty substance. In many secreting glands we found a contrast between the cells in the state of secretion and such as are not secreting, the former showing the intracellular network open, owing to the greater amount of interfibrillar substance undergoing the metabolic change, the latter possessing a more "granular" aspect, *i. e.* the network being much closer. And the same relation we find to obtain also in the sebaceous glands; for the peripheral cells with a dense intracellular network ("granular" protoplasm) bear to the more centrally situated cells—those containing an open network and a fatty interfibrillar substance—evidently the relation of a non-secreting to secreting cells of other glands.

The epithelial cells lining the alveoli of the Meibomian glands of the eye-lids are in every respect analogous to those of the ordinary sebaceous glands; it is, therefore unnecessary for me to enter into details, as I should have only to repeat what I stated just now with regard to the latter glands.

In the embryo at an early stage the alveoli of both ordinary sebaceous and Meibomian glands contain only "granular" cells, *i. e.* cells in which no fatty matter is yet contained in the intracellular network, hence the great closeness of this latter.

The question might be asked, whether in the process of secretion the substance secreted is directly derived from the intracellular network or only indirectly so, *i. e.* from the interstitial substance contained in its meshes?

From what I have repeatedly stated on the occasion of the submaxillary, the mucous and sebaceous glands, the reader will, I think, have come to the conclusion that it is the interfibrillar substance which becomes increased in amount and converted into the matter that is to be secreted, and not the intracellular network itself. This latter is not used up, therefore, during secretion, in the sense in which, for instance, Heidenhain and Lavdowsky assumed it to be, but only alters its arrangement in such a

manner that its meshes become wider. It is, however, quite probable that the interstitial substance is a product of the intracellular network.

(*b*) The epithelial cells lining the sweat-gland tubes—I refer to the coiled part, not the duct—is in sections of skin, hardened in a mixture of chromic acid and spirit, or also spirit alone, the former being however preferable, composed of a substance which is distinctly longitudinally striated. This striation, when examined with a high power, is seen to be due to the intracellular network consisting prevalently of longitudinal fibrils. This appearance is, however, presented chiefly by the inner portion of the cell substance; the other part, containing the nucleus, is of a more uniformly "granular" aspect, *i.e.* the network possessing a uniform dense arrangement. The nucleus is spherical, and contains a uniform network; in some instances I see traces of a "nucleolus" (see fig. 11 of Pl. VII).

Skin of sheep and pig is on account of the large size of the sweat glands a very good object.

The same change of shape of the cells that I have mentioned on the occasion of Lieberkühn's crypts, dependent on the change of lumen of the gland tube, may be noticed also here. Thus I measure in sweat-gland tubes of skin of ear-lobe of pig as the mean:

0·05 mm. the diameter of the whole tube, including its membrana propria,
0·019 mm. the diameter of lumen,
0·01 mm. the height of the lining epithelium,
and about 0·005 mm. the thickness of muscular coat and membrana propria (see fig. 11).

In another instance I measure:

0·076 mm. the diameter of the whole tube,
0·03 mm. the diameter of lumen,
about 0·005 mm. the height of the lining epithelium,
and about 0·002 mm. the thickness of both muscular coat and membrana propria together.

We find, therefore, in the latter instance in a tube with a greatly distended lumen (0·03 mm. as against 0.019 mm. of the former case) an epithelium correspondingly shortened (0·005 m. as against 0·01 mm. of the former case).

November, 1878.

POSTSCRIPT.

THE foregoing paper was in print when Professor Flemming's last memoir—"Contributions to the Knowledge of Cells, &c."—appeared in the 'Archiv f. Mikrosk. Anat.,' Band xvi, p. 302. This memoir, which is of considerable length, records many important observations regarding the structure of cells and nuclei and the phenomena of cell-division.

Flemming's views on the structure of cells and nuclei, and the relation of the two, do not in some respects coincide with those expressed by me in Part I of this paper (see this Journal, Vol. XVIII, p. 315), and also in the present Part II. It is not possible for me to enter here into a detailed discussion of those differences, for the reason that this important subject could not receive full justice in a short paragraph, and chiefly because, in the third and concluding part of this paper, I shall have opportunity to return to the subject. But I will at once here state my dissent from Flemming in two important points:

a. Professor Flemming, on p. 335, says that the network that I described (in Part I of my paper) of the nuclei of stomach and mesentery of newt, after treatment with 5 per cent. chromate of ammonia, does not quite correspond to the network seen by him in the nuclei of Salamandra in the fresh state, and is therefore, in its totality, not to be regarded as a preformed structure.

On the same page (335) he also says that the nuclei delineated in many of my figures (see Plate XVI of this Journal, July, 1878), are knobbed and distorted, and this he regards as additional proof for his above statement. I see from this that Professor Flemming has looked at my figures and read my text with only passing attention, for in that Plate (XVI) I have delineated, and in the text I have described, the nuclei as oval sharply outlined structures, with a smooth surface. Of a knobbed or distorted state I have figured or said nothing. In a very few instances the nucleus is slightly knobbed, *e. g.* in the dividing nucleus of unstriped muscle fibres of the mesentery of newt (l. c., p. 332). I also find that Professor Flemming describes (on pages 307 and 319 of his memoir) a similar condition of nuclei of developing Salamandra in the perfectly fresh and living state.

b. As far as I am able to understand Professor Flemming's observations and arguments on the structure of the nucleus during life and after reagents, it comes to this, that during life some nuclei show nothing of a network or of anything else, being in some instances not visible at all; others show a network more or less imperfectly, with dots and large par-

ticles—nucleoli. Different reagents demonstrate in the nucleus a network and nucleoli with varying distinctness, and it is a question whether what these reagents reveal are partly or wholly artificial products. Flemming suspects the chromates especially as liable to produce artificial products; dilute chromic acid and picric acid, on the other hand, he has great faith in, although reading his observations with bichromate of potash on fresh blood-corpuscles of Salamandra (p. 336), the reader, I think, will come to a conclusion, viz. that bichromate of potash is a very good reagent to demonstrate the intranuclear network, which conclusion is opposite to that arrived at by Flemming himself.

That many things, although not visible in the perfectly fresh state, but only after treatment with reagents, are nevertheless preformed structures, is a proposition which it is unnecessary to prove in the present state of histological science; the whole progress of modern histology contains that proof.

A thing is not visible at all, or only indistinctly so, in the living and fresh state if its refractive index does not differ from the parts surrounding it; after adding hardening reagents many structures are brought out with greater or less distinctness. But there are certain minute structures which have been and can be demonstrated only with certain particular reagents. I remind the reader of the results obtained by Max Schultze with perosmic acid, by v. Recklinghausen with nitrate of silver, by Cohnheim with chloride of gold, &c., then of the different dyes which are used in histology on account of their selective power.

The cornea, carefully cut out and quickly placed under the microscope, shows absolutely no structure; of the different layers of epithelium on the anterior surface, of their nuclei, of the corneal corpuscles and the lacunæ in which they are placed, of the innumerable fine nerves underneath the epithelium, we see nothing, or next to nothing. After the lapse of some time the cornea shows the outlines of some of the epithelial cells, and in some of these we perceive faintly the outlines of the nuclei. If we add a hardening reagent, such as a chromate, chromic acid, or any other acid, alcohol, &c., we at once see all the epithelial cells and their nuclei very well defined; the lacunæ in which the corneal corpuscles lie, and these latter, as well as the fine nerves, are seen very imperfectly and only in a few places. But when treating the cornea, after Recklinghausen, with nitrate of silver, we demonstrate the lacunæ and their canals, and when using Cohnheim's chloride of gold we trace with ease

the branched cells and the nerve fibres in their finest ramifications.

These examples can be multiplied from every book or journal of the present day containing papers on animal histology.

What I wish to point out is that a structure that is very indistinctly or perhaps not at all discernible in the perfectly fresh state, but becomes *very sharp and well marked after a particular reagent*, need not necessarily be an artificial product; if this same structure can be shown also with other reagents, although not so well defined, we are quite justified, I think, in regarding it as preformed, and not as an artificial product.

Now, as regards the intranuclear network. What I described in Part I of my paper, chiefly with the aid of chromate of ammonia, coincides with what is possible to make out in the fresh state, and after other reagents (see my Part I, p. 321), *e. g.* Müller's fluid, bichromate of potash, osmic acid, spirit, &c., with this difference, that in the specimens prepared successfully with chromate of ammonia, there are here sometimes failures on account of the elements swelling up and becoming quite transparent, but the appearances are infinitely more regular and much better defined than with other reagents.

The exquisitely beautiful honey-combed network in the nuclei of the endothelial and connective-tissue cells in the mesentery of newt, prepared *successfully* with 5 per cent. chromate of ammonia, the rich branching, the minute structure of these cells, and of the unstriped muscle fibres, are brought out with a clearness and delicacy not reached by any other reagent with which I have treated that membrane.

The observations which I have recorded in the present Part II prove the correctness of the deductions stated in Part I as regards the structure of cells and nuclei. In studying the epithelial and gland-cells of mammals, besides examining them in the fresh state, I have had occasion to compare the appearances obtained by the use of different reagents, as stated in the foregoing pages—and because the appearances were found similar or identical they were accepted as denoting a preformed structure. If one appearance is brought out with greater distinctness with chromic acid than with another reagent, I do as Professor Flemming does, viz. I give it the preference in the examination, but I should not reject spirit, chromate of ammonia, bichromate of potash, &c., if in any other instances the appearances are better defined by one of

these reagents than they are in the fresh state or by chromic acid.

Flemming, in the above paper, expresses dissent from the view of a connection between the intracellular and intranuclear networks; the same opposition is expressed by W. Schleicher in a paper on the division of cartilage-cells ('Archiv Mikrosk. Anatomie,' p. 261), both he and Schleicher declaring the nucleus to be something quite separate and independent of the cell-substance. From my own experience as described in the foregoing pages, I must most decidedly oppose this separation of nucleus and cell-substance, and I would particularly draw attention to the remarkable observations of Stricker ('Sitzungsb. d. k. Akad. d. Wiss.,' June, 1877) on colourless blood-corpuscles of frog and newt. Stricker ascertained the contractility of the intranuclear network and the continuity of this with the cell-substance, as well as the important fact that the membrane of the nucleus disappearing, its network becomes fused with the cell-substance, and *vice versâ*, the membrane appearing a part of the cell-substance becoming enclosed in it as nucleus. *The nucleus is therefore a portion of the cell-substance specially differentiated by the presence of a membrane.*

I have repeated the observations of Stricker on the large pale, and also on the small uninuclear corpuscles of newt's blood on the warm stage, and I can fully confirm his statement that the internuclear network, especially of the latter, is contractile, and that the substance of the nuclei of the former becomes fused with the cell-substance, this membrane disappearing on one side or the other. The cell-substance is a minute network of varying distinctness.

On the APICAL *and* ORAL SYSTEMS *of the* ECHINODERMATA.

By P. HERBERT CARPENTER, M.A., Assistant Master at Eton College. Part II.

IN a previous paper[1] I have discussed at some length the modifications of the Apical System of the Echinoderms in the various members of the group. I now propose to treat the Oral System in the same manner, commencing, as before, with the Crinoids, in which order it reaches a very high degree of development.

After the disappearance of the ciliated bands encircling the echinopædium of *Comatula*, its anterior extremity becomes flattened and depressed in the centre. The raised external rim of this depression exhibits a division into five crescentic lobes, the oral lobes, which are situated *interradially*. Opposite to the intervals between them are five azygos tentacles marking the positions of the future radial water-vessels, while interradially, opposite to each of the oral lobes, is a pair of short tubular tentacles, borne like the azygos one upon the water-vascular ring.

The oral lobes are supported by the oral plates, which in the earliest condition of the skeleton are situated directly above, but in close juxtaposition to the basals. But as the body increases in size, its equatorial portion, *i.e.* the band between the upper edges of the basals and the lower edges of the orals rapidly enlarges. During this enlargement the oral plates maintain their original position, so that they become completely separated from the basals by the growing equatorial band, in the dorsal portion of which the radial plates appear resting upon the basals. The orals are finally left as a circle of five separate plates, each enclosed in its lobe of perisome, on the centre of the new ventral or upper surface of the larva, surrounding the mouth and enclosing the circlet of ten interradial tentacles. This ventral surface gradually widens as the radials enlarge and extend outwards, carrying the perisome with them, to form the bases of the arms. The "anal" plate appears in one of the interradial spaces of the new formed disc, between the upper portions of two of the first radial plates. The position of the anus indicates that of the blastopore, which was primitively nearly in the centre of the ventral surface of the Gastrula, and also a point in the plane of division between the right and left larval antimera; for this plane is occupied by a circular

[1] This Journal, Vol. XVIII, pp. 351–383.

mesentery, which is formed by the fusion of the walls of the two peritoneal cæca, and supports the rectum.[1] Very early, however, there is a general forward movement of all the ventrally placed structures, namely, the depression marking the position of the future mouth, the water-vascular sac, the oral cœlom, and the blastopore. These all take up a new position at the anterior end of the Crinoidal axis (transverse axis of the Gastrula), and it is here that the ventral or actinal surface of the future *Comatula* begins to appear, in a plane very considerably inclined to that of the ventral surface of the Gastrula.

This rudimentary actinal surface primitively consists of nothing but the area occupied by the oral plates, together with the bases of the arms. But as the digestive tube increases in length and acquires an anal orifice, the radials spread out very much, so as to extend the base of the cup; while the single anal plate, originally interposed between two of them, begins to be lifted out, as it were, from this position, as it is attached more to the growing visceral mass than to the neighbouring plates.

At the same time the diameter of the oral circlet, still embracing the ring of oral tentacles, continually decreases in proportion to that of the disc or visceral mass, as the size of the latter is increased by the development of the alimentary canal.

Finally, the oral circlet detaches itself from the summit of the radials on which it previously rested, and is *relatively* carried inwards by the great enlargement of the circle formed by them. The space between the two series is now filled in only by the membranous perisome of the above-mentioned equatorial zone, over which the ambulacral grooves extend themselves, passing outwards from the circum-oral region between the oral valves towards the growing arms.

The diameter of the visceral mass continually increases, so that it extends nearly as far as the bifurcation of the arms, and the oral circlet is thus separated by a much wider interval from the periphery of the disc. It is in this outer ring that the anal funnel is situated, the anal plate which it bears on its outer side being altogether lifted out from between the two radials which it originally separated. In some *Palæocrinoidea*, however, it retains its primitive position within the radial circlet.

I have already mentioned[2] that in most recent Crinoids the orals of the larva are completely resorbed, so that no

[1] Götte, loc. cit., pp. 591, 601, 609.
[2] Part I, p. 355.

e of them is visible in the adult, and the single anal ...e undergoes the same fate. The orals persist, however, ...izocrinus and *Hyocrinus*. Wyville Thomson[1] describes ...in the latter genus (fig. XII) as five triangular valves ..., which close over the central mouth so as to form a very

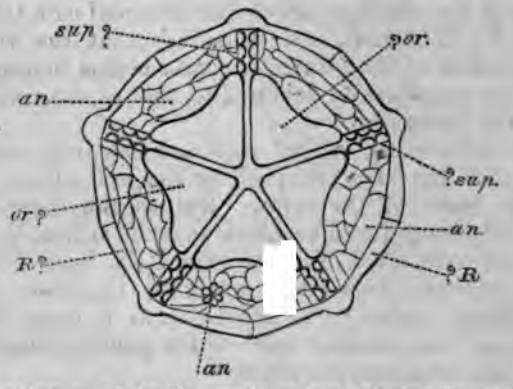


FIG. XII.—Diagram of the disc of *Hyocrinus* (adapted from a figure of Sir Wyville Thomson's). *An.* Anal tube. *an.* Anambulacral plates. *sup.* Superambulacral or marginal plates = Saumplättchen. *or.* Oral plates. *R.* Radials.

perfect five-sided pyramid. The peripheral part of the disc is paved with closely-set plates (*an*), the outer ones of which are in contact with the broad thin radials (*R*). The width of this plated marginal zone surrounding the oral valves is extremely slight, being only about one quarter of the total diameter of the disc. The anal opening is near the edge of this zone, at the end of a short, plated, interradial tube (*An*). The plates on the ventral surface of the disc, to which Müller[2] gave the name of *anambulacral*, are very completely developed in many *Pentacrini*, as in *Hyocrinus*. Many of them are perforated by the water-pores which place the body-cavity in communication with the exterior.

In *Rhizocrinus*, and in the *Comatulæ*, these anambulacral plates are less constant in their appearance than in *Hyocrinus* and *Pentacrinus*. But in one or two tropical *Comatulæ* they are very marked, and pass over at the margin of the disc into a complete interbrachial plating, which covers the surface of the perisome between the five rays, beyond the level of the second radials.

All this anambulacral system forming the peripheral part

[1] 'Journ. Linn. Soc.,' xiii, "Zoology," p. 53.
[2] 'Bau der Echinodermen,' p. 63.

of the "tegmen calycis" is developed out of the narrow equatorial zone of perisome intervening between the oral and basal circlets of the young Pentacrinoid. It does not seem to be present in the *Palæocrinoidea*, the solid vault of which, as pointed out by Wachsmuth,[1] is in no way homologous with the ventral perisome of the recent Crinoids. Allman[2] has already pointed out that in many members of this group there is a system of plates in the centre of the vault, which is nothing but a more or less extensive development of the simple oral system of the young *Comatula*. Wachsmuth,[3] who has studied the complicated arrangement of these plates with much care, has somewhat unfortunately termed them "apical," a name already applied by previous writers to the plates which form the calyx at the opposite pole of the body. In the simplest condition of these so-called apical plates, as shown in genera which have but a few vault pieces, there is a large central plate surrounded by six others, viz. four large interradial ones of equal size, and two smaller ones, also interradial, which are separated by the anus, and together correspond to a single larger one. Wachsmuth has found these "apical" plates in the families *Actinocrinidæ*, *Platycrinidæ*, *Rhodocrinidæ*, *Melocrinidæ*, and in a few isolated genera, including *Cyathocrinus* and *Synbathocrinus*, in which last they are represented by a number of small plates; and he states that they "cover the central opening of the Blastoids, and can be traced in many of the Cystideans."[4] They occupy a central position in the vault, where there is much reason to believe in the presence of a subtegminal mouth; and they are very largely developed in young specimens, from which, as well as from other considerations, Wachsmuth infers "that they were the first solid parts developed on the ventral side in young Crinoids."

Although the central plate was unknown to Allman, there can, I think, be little doubt that the six (practically five) peripheral plates are comparable to the orals of the young *Comatula* in the manner suggested by him. These plates surround and support the walls of the tentacular vestibule, into which thelarval mouth opens (fig. XIII *lp'*), but it does not acquire a communication with the exterior until a comparatively late stage of development. Götte's sugges-

[1] "Notes on the Internal and External Structure of Palæozoic Crinoids," 'American Journal of Science and Arts,' vol. xiv, 1877, pp. 123, 190.
[2] Loc. cit., pp. 245-251.
[3] Loc. cit., p. 187.
[4] Loc. cit., p. 189.

tion[1] that many *Palæocrinidæ* and *Cystidea* have remained permanently in this condition appears to me to be an exceedingly happy one, as far as the former group is concerned,

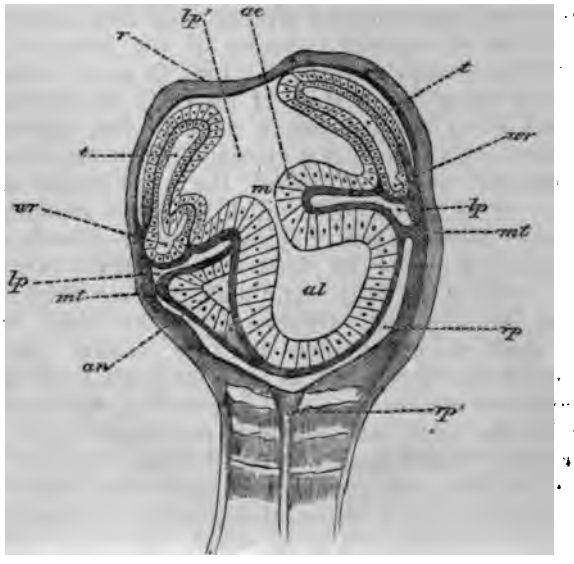


FIG. XIII.—Section through a Pentacrinoid with a closed tentacular vestibule, the mouth not having yet broken through to the exterior. (After Götte.)[2] *ae*. Ambulacral epithelium. *al*. Alimentary canal. *an*. Rudiment of anus, marking the position of the blastopore. *lp*. Posterior division of the left peritoneal sac, from which the subtentacular canals are derived. *lp'*. Its anterior division, forming the tentacular vestibule. *m*. mouth. *mt*. Mesentery, separating the cavities of the right and left peritoneal sacs. *r*. Roof of the tentacular vestibule = vault of *Palæocrinoidea*. *rp*. Right peritoneal sac, giving rise to the greater part of the body cavity. *rp'*. Its posterior extension into the developing stem. *t*. Tentacles. *wr*. Watervascular ring.

though I do not think it applicable to the Cystids with grooves on the "vault." It gives us a complete explanation of their subtegminal mouth, the presence of which has been so successfully demonstrated by Wachsmuth,[3] in accordance with Schultze's suggestion.[4] Thus, in many Palæozoic genera the mouth is permanently subtegminal, while in the more modern forms it is only temporarily so during the

[1] Loc. cit., p. 637.
[2] See Plate xxvi, fig. 19, of Götte's paper.
[3] Loc. cit., pp. 116, 120.
[4] Loc. cit., p. 7 (119).

Pentacrinoid stage of development, and ultimately opens directly to the exterior. Wachsmuth's descriptions of some natural casts of the structures below the vault of the *Actinocrinidæ* correspond in a most striking manner with what Götte has shown to be the condition of the young *Pentacrinoid*.

He describes the centre of radiation for the concealed ambulacra as a variously shaped space or plane, surrounded by a furrow. The middle of this space is frequently occupied by a small opening, or by a little cone indicating an aperture leading to the inner cavity. This little central opening, situated at the upper end of the vertical axis below the vault, occupies, as Wachsmuth points out, the same position as the mouth of *Antedon* occupies in the peristome (fig. XIII, *m*). Now, this lip or peristome is nothing more than the floor of the tentacular vestibule, which is closed till late in the Pentacrinoid stage (fig. XIII, *r*), but ultimately opens to the exterior; while the corresponding space in *Actinocrinus* remains permanently closed and covered in by the system of actinal plates, namely, the single central one with the six (=5) orals around it.

Götte's suggestion also helps us to understand why there is no central actinal plate developed inside the oral circlet of *Comatula*. For it would be situated precisely at the point where the rupture of the peristome occurs that places the tentacular vestibule, into which the true mouth opens, in communication with the exterior. Were it developed it would only be in the way, and have to undergo resorption to a greater or less extent, just as the central abactinal plate of many Urchins is more or less completely resorbed after the appearance of the anus.

We find, then, that the oral system of the *Palæocrinoidea* consists of a central actinal plate, around which six (= five) oral plates are disposed. The resemblance between this arrangement and that of the central abactinal plate, with the five basals disposed interradially around it, strikes one at once, and we thus find a complete correspondence between the primitive conditions of the skeletal elements developed around the two peritoneal sacs of the Crinoid larva. On the actinal as well as on the abactinal side there is a single central plate surrounded by five others, which are interradial in position. There is, however, no known Crinoid in which we find this primitive condition persisting, even as an embryonic feature. For the central actinal plate is limited to the *Palæocrinoidea*, while in all but *Holopus* (so far as is known) the rudiments of the stem make their appearance at

a very early stage of development, simultaneously with those of the other plates of the skeleton, and (as I believe) carry away the central abactinal plate from the neighbourhood of the basals. A suggestion essentially similar to the one just made has already been put forward by Wachsmuth,[1] who regards the central abactinal plate as the basis, a view which, as I have already endeavoured to show, is no longer tenable.[2] Wachsmuth also compares the interradial peri-

	Abactinal System.		Actinal System.
	Wachsmuth.	*P. H. Carpenter.*	
Central Plate.	Basis.	Central Plate at end of stem.	Central Plate.
Peripheral Plates. *Interradial.*	Parabasals or Subradials.	Basals.	Orals.

pheral plates (orals) of the actinal surface to the so-called parabasals or subradials of the abactinal system, which "were undoubtedly the *first developed* parts of the dorsal side, and the parts which are the most highly developed in the Cystideans." It will be noted how this passage strengthens the arguments which I have already brought forward in favour of the view that the so-called subradials are the true basals of those Crinoids in which they occur.

The diameter of the visceral mass of the Pentacrinoid is so slight that the orals are sufficient to cover it in completely on the ventral side. But in the *Palæocrinoidea* it is not only absolutely, but also relatively, much larger, so that the oral or "apical" system alone is insufficient to cover it.

Accordingly we find that the "apical" plates do not make up the whole of the vault of the *Palæocrinoidea*, but "there are other summit plates following a radial direction, which are either attached to the apical pieces or separated from them by a belt of small polygonal plates," while the intermediate spaces between these radial areas are occupied by the interradial plates of the vault. The number and arrangement of these plates vary greatly in different species, accord-

[1] Loc. cit., p. 189.
[2] Part I, this Journal, Vol. XVIII, pp. 360, 370, 371.

ing to the number of primary arms that spring out directly from the body. As a general rule, according to Wachsmuth,[1] "the summit plates increase in proportion to the number of primary arms of a species, in the same manner and on the same principle as the plates of the dorsal side."

We find then, that in the Palæocrinoidea there is an almost complete correspondence in the skeletal developments on the actinal and abactinal surfaces of the body.[2] The centre is occupied in each case by a single plate, surrounded by five others, which are situated interradially. But the first and second radials of the abactinal pole appear to be unrepresented on the actinal surface. Peripherally, however, there is again a very close correspondence in the arrangement of the plates on the two surfaces.

The vault of the *Palæocrinoidea* appears to be something *sui generis*, and altogether unrepresented in our more modern forms. According to Wachsmuth,[3] with whom I entirely agree, "it cannot in the remotest degree be homologised with the ventral peristome" of the recent Crinoids. "It forms a continuation of the radial and interradial series of the dorsal side, and serves merely as a covering and protection for the organs underneath." There is every reason to believe that these were of essentially the same character as in the recent Crinoids, namely, ambulacral grooves with the radial water-vessels underlying them. The ambulacra of a *Comatula* or *Pentacrinus* are continued from the arms on to the disc, where they converge towards the peristome; while in the *Palæocrinoidea* they enter the cavity of the vault by apertures at the base of each arm, and continue their centripetal direction as subtegminal channels along the inner surface of the vault. These channels were first discovered in *Actinocrinus* by Huxley and Billings,[4] and are "floored by a series of plates which form an elongated arch under them." Alternating with the upper edges of these plates there are found, in good specimens, two rows of minute quadrangular interlocking plates, longitudinally arranged so as to cover the tubes. Hence, under the vault these canals must have been "formed of two rows or pieces below (*subambulacral*) and two above (*superambulacral*), all alternately arranged." By Wachsmuth, as by Meek and Worthen,[5] they are

[1] Loc. cit., p. 187.
[2] See Addenda, No. 3, on p. 204.
[3] Loc. cit., p. 190.
[4] "On the Cystideæ of the Lower Silurian Rocks of Canada," 'Geographical Survey of Canada,' decade iii, p. 27.
[5] "Notes on some points in the Structure and Habits of the Palæozoic Crinoidea," 'The Canadian Naturalist,' 1869, pp. 443, 444.

regarded as continuations of the ambulacral grooves of the arms.

In these *Actinocrinidæ* the structure of the arms is not yet known; but in *Cyathocrinus* the brachial ambulacra are bordered by a row of interlocking triangular plates, which Wachsmuth[1] compares to the "marginal plates" in recent Crinoids. They rest on an outer row of plates longitudinally arranged and attached to the arm-joints. This double series of alternating plates extends beneath the vault of *Cyathocrinus*, but the subambulacral plates appear to be absent from the grooves of both vault and arms. We thus find that the ambulacra of the Crinoids may be surrounded by three sets of plates—(1) An upper series, present in both *Cyathocrinus* and *Actinocrinus*. (2) An under series present in *Actinocrinus* only. (3) A lateral series, present in *Cyathocrinus* only (so far as we yet know). Wachsmuth has already pointed out the homology of the upper series (1) with the marginal plates in recent Crinoids (fig. XIV *sup*), but he has overlooked the fact that both the other series (2, 3) are also represented, at any rate in the disc of *Pentacrinus caput-meduse*. According to Müller[2]—

"An den Armen und Pinnulae beschränken sich die kalkigen Bildungen auf der Ventralseite bloss auf die Saumplättchen der Ambulakralrinnen. Am Kelch dagegen sind die Ambulakralrinnen noch ausser den Saumplättchen durch kalkigen Bildungen unterstützt. Diejenigen Plättchen welche den Rand der Ambulakralrinnen bilden, haben eine wallartige Erhöhung und dienen den Ambulacra Sowohl fur Einfassung als fur Stütze der aufgerichteten Saumplättchen; man kann sie Seitenplatten der Ambulacra nennen. . . . . Unter der weichen Auskleidung der Rinne liegen auch noch Täfelchen."

This last set of plates (fig. XIV *sub*) was termed *subambulacral* by Müller, and there can, I think, be little doubt that

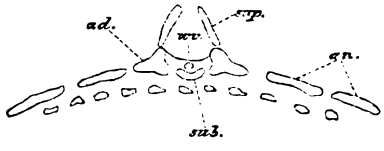


FIG. XIV.—Diagram of the plates surrounding the ambulacra on the disc of *Pentacrinus*. Slightly altered from J. Müller. *ad.* Adambulacral (3). *an.* Anambulacral. *sub.* Subambulacral (2). *sup.* Superambulacral = marginal plates or "Saumplättchen (1). *wv.* Water vessel.

it represents the double row forming the floor of the subtegminal galleries of *Actinocrinus*.

[1] Loc. cit., p. 122.
[2] "Bau der Echinodermen," loc. cit., p. 57.

These galleries enclosed between the super- and sub-ambulacral plates lodged, I believe, not only the ambulacral grooves but also the water vessels. In the recent Crinoids and Starfishes these two are separated in each arm by a membranous partition containing several structures, which need not be considered here. Around the mouth the grooves expand into a peristomial area, beneath which is the water-vascular ring. The subtegminal galleries of *Actinocrinus* open into what Wachsmuth[1] calls an "annular vessel," composed of minute interlocking plates, and resting on the convoluted digestive organ. This ring has five small openings leading into the subtegminal galleries, and alternating with these on the lower side of the ring there are five other small openings, which Wachsmuth supposes to have been "in connection with organs of the interradial system (communicating perhaps with a circulatory system)."

This "annular vessel" represents, I believe, both the peristomial area of our recent Crinoids and the subjacent water-vascular ring, which is only separated from it by membrane. It is easy to understand the nature of the interradial openings on its floor. I imagine them to be the openings of the small tubes which, in the recent Crinoids, depend from the water-vascular ring into the body cavity. According to Ludwig,[2] they open freely into it, and are to be regarded as afferent vessels serving for the introduction of water into the ambulacral system, and therefore as collectively representing the sand canals of the other Echinoderms. In the Ophiurids, however, there is not only a sand canal extending from the madreporite to the water vascular ring, but depending from this ring into the body cavity there are a number of apparently cæcal diverticula, the *vasa ambulacralia cavi* of Simroth.[3] The resemblance between these and the so-called "Steincanäle" of the Crinoids is very close, as pointed out by Huxley[4] and the two sets of tubes appear to me to be truly homologous. Like Greeff,[5] I am not altogether satisfied (*pace* Ludwig) that they actually open into the cœlom in *Comatula*, while Simroth believes them to be blind in *Ophiactis*. Hence I cannot quite agree with Ludwig's view of their character.

[1] Loc. cit., p. 118.
[2] "Crinoideen," loc. cit., p. 48.
[3] "Anatomie und Schizogonie der *Ophiactis virens*, Sars.," Zeitsch. f. wiss. Zool.,' xxviii, p. 456.
[4] 'The Anatomy of Invertebrated Animals,' p. 586.
[5] "Ueber den Bau der Crinoideen," 'Marburg Sitzungsberichte,' No. 1, 1876, p. 22.

For if they *do* functionally represent the sand canals of the other Echinoderms, why do they coexist with the sand canal in the Ophiurids? Whatever their nature, however, they were present in *Actinocrinus*, but greatly reduced in number. In both *Antedon* and *Actinometra* they are extensively developed; but Ludwig has found that in *Rhizocrinus*[1] there is but one in each interradius, and I imagine that this was also the case in *Actinocrinus*.

From what has been said above, it will be evident that I entirely accept Schultze's hypothesis of a subtegminal mouth in the *Palæocrinoidea*, which has been attacked by Billings,[2] but ably defended by Wyville Thomson,[3] Lütken,[4] Meek and Worthen,[5] and lastly, by Wachsmuth.[6] The last mentioned observer says that "The little central aperture located at the upper end of the vertical axis, occupied on the casts, and hence below the vault of these Crinoids, exactly the same position that the internal mouth of *Antedon*, occupies at the peristome, while the position of the string-like ridges (in case they represent passages, as I can hardly doubt) is analogous with that of the open food grooves of recent Crinoids." I cannot but believe that Wachsmuth's explanation of these ridges is the true one, though it is by no means necessary that they should represent closed passages. In many recent *Comatulæ* it is exceedingly common for the ambulacral grooves of the disc to be considerably raised above the interambulacral areas, so as to present an appearance of "elevated rounded ridges almost like strings overlying the surface," just as Wachsmuth describes in his casts.

Billings' objections to the theory of a subtegminal mouth in the *Palæocrinoidea*, appear to me to be the result of a confusion of terms, and of a want of acquaintance with the anatomy of recent Crinoids. In the first place he described two quite distinct and separate structures under the single name of "ambulacral groove." On p. 20 of the Decade, he used this term in the sense in which it was used by Müller, namely, to denote the furrows radiating outwards from the

[1] Loc. cit., p. 118.

[2] "Notes on the Structure of the Crinoida, Cystidea, and Blastoida," 'Canadian Naturalist,' 1869, pp. 277—283, and 1870, pp. 191—198.

[3] "On the Structure of the Palæozoic Crinoids," 'Nature,' vol. iv, pp. 496—497.

[4] "Notes on Lovèn's Articles on *Leskia mirabilis* and on *Hypoxome Sarsii*" 'Canadian Naturalist,' 1868, pp. 439—441, and 1869, pp. 267—269.

[5] Loc. cit., pp. 441—446.

[6] Loc. cit., pp. 116—120.

mouth over the ventral perisome of the disc and arms. These grooves are altogether outside and above the radial trunks of the water-vascular, blood-vascular, and generative systems, which are covered in by the ventral perisome bearing the grooves. Billings, however, supposed that "the grooves of the arms are occupied" by these tubes, and spoke of them as continued into the interior of the vault by notches in the first radial plates. Here he confounded the supra-tegminal ambulacra with what I have elsewhere described as the "ventral radial furrow," occupying the middle line of the skeleton. All the soft parts of the arm are situated above, this skeletal groove, but beneath the ambulacral groove, which Müller was accustomed to call the "*Tentakelrinne*," in distinction to the skeletal one which he termed the *Armrinne* "worin Weichtheile gelegen sind."[1] Billings, however, confounded the two, and because the vascular and generative tubes which lie above the armgroove (being partially contained in it) do not communicate with the stomach, he supposed it to have been impossible for food particles to gain access to the interior of the animal from the arms of a Palæocrinoid, which, as far as we know, resembled in these points the arms of a *Comatula* or *Pentacrinus*. Here he quite overlooked the fact that the ventral perisome covering the arm of a recent Crinoid bears the true ambulacral groove, along which, and therefore *above* the vascular trunks, the food particles travel towards the mouth. The remains of these brachial ambulacra are found in the *Palæocrinoidea*, and they undoubtedly entered the vault by the ambulacral openings at the bases of the arms, which Billings himself discovered, together with and above the vascular trunks. Billings[2] supposes that the ambulacra of the Crinoids and Asterids *contain* the vascular, nervous, and generative trunks, "which are situated on the outside of the animal, and communicate with the interior *through the mouth*." Consequently he regarded this aperture as having three functions, being (1) the oral, (2) the ovarian, and (3) the ambulacral opening, and he therefore compared it with respect to the last two, to the openings at the arm bases of the *Palæocrinoidea*. These were undoubtedly both ovarian and ambulacral, as the generative organs and the water-vessels passed through them to reach their respective circumoral centres. The ambulacra of the arms also entered here and converged towards a subtegminal mouth. Billings refused to admit the oral nature of this opening, which he

[1] "*Pentacrinus*," loc. cit., p. 35.
[2] Decade iii, loc. cit., p. 19.

appeared to regard as a central ambulacral orifice, and consequently supposed that on Schultze's theory, "*Caryocrinus ornatus* was a polystome animal, and drew in its food through its six ovarian apertures." To me, as it did to Billings,[1] this certainly does appear "utterly incredible."

Wyville Thomson,[2] Agassiz,[3] and Lütken have laid great stress on the fact that in all the recent Echinoderms the mouth is in the centre of the radial system, and that, therefore, the valvular orifice of the *Palæocrinoidea*, which is situated at the point in the vault behind the radial centre of the ambulacra, cannot possibly be the mouth, but is probably the anus.

Billings admitted the universal connection of the mouth and radial centre in the recent Echinoderms, but, being firmly convinced that the valvular orifice was oro-anal in function, he asserted[4] that "in at least a large proportion of the palæozoic Crinoids the mouth was altogether disconnected from the radial system," this being evident from "simple inspection." He did not, however, make it clear how "simple inspection" can demonstrate the oral nature of the valvular orifice. He supposed the same to have been the case in the Cystids, in which, like De Koninck[5] and Gray,[6] he regarded the "ovarian pyramid" of Von Buch as oral in function; while the small opening near the centre of the upper part of the body, from which the ambulacra radiate, was called by him an ambulacral orifice, through which "the vessels of the aquiferous system and of the organs of reproduction which were situated in the grooves of the arms communicated with the interior." Lovén[7] has entirely adopted Billings' views, but Agassiz, like Lütken and Wyville Thomson, has opposed them strongly, and reaffirms the views of Volborth and Müller, that the mouth is at the radial centre of the ambulacra, and is, in fact, the minute ambulacral orifice of Billings.

It appears to me that there can be no doubt about this so

[1] 'Canadian Naturalist,' 1871, p. 137.

[2] "On a New Tertiary Group of Echinodermata," 'Edinburgh New Philosophical Journal,' vol. xx., p. 1 (?).

[3] "Note on Lovén's Article on *Lepidocentrus novidiolus*," 'Annals of the Lyceum of Natural History,' vol. ix., pp. 246—248.

[4] 'Canadian Naturalist,' 1869, p. 273.

[5] Loc. cit., pp. 55 *et seq.*

[6] 'Catalogue of the Recent Echinida or Sea Eggs in the Collection of the British Museum,' 1855, p. 68, t. 4, f. 4.

[7] Decade iii., p. 15.

[8] "Om *Lepidocentrus novidiolus*," Gray, 'Öfversigt af Kongl. Vetenskaps-akademiens Förhandlingar,' 1867, No. 5, pp. 436—440.

far as *Sphæronites* is concerned, this being the type taken by Lovèn for comparison with the other Echinoderms. Wyville Thomson, indeed, regards these forms as "Crinoids, or a parallel group;" and I imagine their ventral surface to be in every respect homologous with that of our modern Crinoids, more especially of *Actinometra*. In this genus the ambulacra form an open horseshoe-shaped curve, very much as in *Sphæronites*. The mouth is placed in the middle of this curve, but it is often extremely small and inconspicuous, being merely a short and narrow slit in the peristomial area.

I have often experienced great difficulty in finding it even in spirit specimens, in which the perisome was quite bare; while in dry specimens of such species as *Act. solaris*, in which the anambulacral plating is often very completely developed, I should, like Müller,[1] have altogether failed to find it, had I not known with tolerable certainty, from other considerations, where to look for it. I imagine the Cystids with calycine ambulacra to have resembled, in this respect, such recent Crinoids as *Hyocrinus*, in which there is an extensive anambulacral plating on the disc and minute plates in the marginal leaflets at the sides of the ambulacra. We find precisely the same condition in the so-called recent Cystid, *Hyponome Sarsii*, in which the ambulacra are fringed and overlapped by marginal scales, while the remainder of the ventral surface "is clothed with rather small, thickset, irregular scales;" and it appears to me that Wyville Thomson[2] is right in regarding *Hyponome* as a true Crinoid. According to Lovèn[3] the "absence of any indication of a calyx" tells strongly against this view, but I believe that *Hyponome* is merely the disc of a Crinoid, which has fallen out of its calyx, and that indications of its attachment to a skeleton are seen in the "five broad dichotomous rays on the dorsal surface."[4]

Thus then I regard the vault of the Cystids (at any rate of those with open ambulacra), as quite distinct from the vault of the *Palæocrinoids*, but as homologous with the ventral perisome of our recent Crinoids. This is frequently covered with an extensive anambulacral plating, which is perforated by the small water-pores. In *Pentacrinus* most of the anambulacral plates are perforated in this way, the

[1] "Ueber die Gattung *Comatula*, Lam. und ihre Arten," 'Abhandl. der Berlin Akad.,' 1847, p. 245.

[2] 'Nature,' loc. cit., p. 497.

[3] "On *Hyponome Sarsii*, a recent Cystidean," 'Canadian Naturalist,' 1869, p. 266.

[4] See Addenda, No. 4, on p. 205.

water-pores being very numerous, and in *Caryocrinus*[1] the pores are also numerous, but "nehmen den antiambulacralen Theil des Kelches hinter den Armen bis zur Basis ein." On the other hand, Ludwig[2] has shown that in *Rhizocrinus* there is but one water-pore in each interradial area of the disc, although the plating of the perisome may be very extensive. Water-pores are found in most Cystids, being variously arranged into poriferous or tubular structures, but the distribution of these is very different in different genera. They are usually antiambulacral, as in *Caryocrinus*, but in *Protocrinus* and *Glyptosphærites* they occur between the ambulacra of the ventral surface as in *Pentacrinus*. Billings[3] has attempted to show "the gradual passage or conversion of the respiratory organs of the *Cystidea*, *Blastoidea*, and *Palæocrinoidea* into the ambulacral canal system of the recent Echinoderms." I cannot, however, regard his attempt as successful. This is not the place for a critical examination of his arguments, but I may remark that the pectinated rhombs of the Cystids and the hydrospires of the Blastoids are all interradial, while the water-vascular trunks of the recent Echinoderms are radial in their origin. Further, Müller has pointed out that the homologues of the former in the recent Crinoids are the water-pores of the disc, the existence of which appears to have been quite unknown to Billings; and Ludwig[4] has recently shown the very close resemblance between the structure of the so-called genital clefts of the Ophiurids and the hydrospires of *Pentatremites*, so that there is no occasion to seek for the homologues of the latter in the water-vascular system of the Crinoids or Ophiurids as Billings has done.

The skeleton of a modern Crinoid then, may be regarded as composed of three distinct systems of plates, viz. the abactinal or apical, the actinal or oral, and the intermediate, which is both ambulacral and inter- or anambulacral. These may be developed in very different degrees of complexity, especially in the older forms. Their mutual relations are presented as simply as possible in the modern *Hyocrinus*, while in genera like *Eucalyptocrinus* and *Rhodocrinus*, one or more of these systems is extremely complicated by the extensive subdivision of its primary elements and the development of secondary ones. Lastly, in *Comatula* the oral

[1] 'Bau der Echinodermen,' p. 64.
[2] Loc. cit., p. 118.
[3] 'Canad. Nat.,' 1869, p. 426.
[4] "Beiträge zur Anatomie der Ophiuren," 'Zeitschr. für wiss. Zool.,' Bd. xxxi, pp. 282-285.

and the apical systems, although extremely well developed in the larva, undergo very extensive changes which result in the total disappearance of the oral system, and a considerable modification of the basal element in the calyx. In some tropical species the anambulacral system may reach a high stage of development, but in the British species it is very imperfect even in the larva, and shares the fate of the oral plates by undergoing complete resorption.[1]

I have already endeavoured to determine the homologies of the Crinoidal calyx in the other Echinoderms. Let us now attempt to solve a similar problem with regard to the other elements of their skeleton. The oral system of a Crinoid consists essentially of five plates or series of plates, disposed interradially around the mouth. I have already stated that I have entirely failed to find any traces of these plates in any of Agassiz' figures of Asterid larvæ, and that as far as can be judged from *Metschnikoff's* figures their presence in the Ophiurids is very uncertain.[2] In the Holothurians, however, the oral plates of the Crinoids are very well represented. Kowalewsky[3] figures five large triangular plates around the mouth of the young *Psolinus brevis*, without any trace of a commencing skeleton in any other part of the body. He makes no reference to them whatever, but they seem to persist through life; if not in *Psolinus*, at any rate in *Psolus ephippifer* in which, according to Wyville Thomson, a slightly elevated pyramid of five very accurately fitting calcareous valves closes over the oral aperture and the ring of oral tentacles.

Again, Krohn[4] describes a Holothurian larva in which the border of the blunt and rounded anterior end is "durch 5 vorspringende durchlöcherte Kalkscheibchen in eben so viele Lappen getheilt." Besides these, the whole perisome contains a number of overlapping reticulated plates. These also occur in the *Cucumaria* larva figured by Selenka,[5] but there is no trace of orals, and the plates are smaller than in Krohn's larva, and not in contact.

With regard to the *Echini*, it might seem at first sight rather a hopeless task to attempt to determine the elements of an oral system among the large number of plates which

[1] W. B. Carpenter, 'Phil. Trans.,' loc. cit., p. 471.

[2] See Addenda, No. 5, p. 205

[3] "Beitrage zur Entwickelungs-geschichte der Holthurien," 'St. Petersburg Memoirs,' tome xi, No. 6, fig. 13.

[4] "Beobachtungen aus der Entwickelung der Holothurien und Seeigel," 'Müller's Archiv.,' 1851, p. 347.

[5] "Zur Entwickelung der Holothurien," 'Zeitschr. für Wiss. Zool.,' Band. xxvii, taf. xiii, fig. 28.

cover the buccal membrane of an ordinary Urchin. But in the remarkable form *Leskia* (*Palæostoma*) *mirabilis*, there are only five plates on the buccal membrane. These are large, triangular, and interradial in position, as they alternate with the bases of the ambulacra. Here I believe we have the key to the problem, one which both Gray and Lovèn have attempted to use, and in two different ways, neither of which seems correct when viewed by the light of our present knowledge. In 1851, Gray[1] wrote as follows, respecting *Leskia*: "In the form of the mouth and vent it has considerable affinity with the fossil *Cystidea* of Von Buch, as especially the genus *Echinosphærites*." Some years later, when Billings and others had attempted to show that the so-called "ovarian pyramid" was really the mouth or mouth-anus, Lovèn[2] compared its five valves to those surrounding the mouth of *Leskia*, a point which seemed to give considerable support to Billings' views. On the whole, however, it seems most probable that Agassiz, Lütken, and Wyville Thomson, are right in regarding the ovarian pyramid as anal in function. Agassiz[3] compares its five valves to the five plates which cover the anal opening in many young *Echini*, during a considerable period of their growth, but which ultimately undergo much modification.

Leaving the Cystids for the present and returning to the simpler and more comprehensible recent Crinoids, I think there can be little doubt as to the homology of the oral plates of *Hyocrinus* and of the Pentacrinoid larva of *Antedon*, with the similar and similarly situated plates in the actinostome of *Leskia*. We have seen that the Crinoid skeleton may be regarded as composed of three distinct systems of plates, the apical, the oral, and the intermediate. The latter is developed in an equatorial zone, occupying the larger or smaller area of perisome which gradually appears between the oral and apical systems of the larva. A general homology (irrespective of details) between the apical systems of Crinoids and *Echini* is now universally admitted; and if, as I have endeavoured to show, the five oral valves on the actinal membrane of *Leskia* are homologous with the oral circlet of a Crinoid, then the coronal plates of the Urchin must represent those developed in the equatorial zone of the Crinoid. A still closer resemblance in matters of detail will be pointed out further on.

In some young spatangoids (*Brissopsis*) the actinostome is

[1] Loc. cit., p. 63.
[2] "Om *Leskia mirabilis*," loc. cit., pp. 436—440.
[3] Note on Lovèn's article on *Leskia mirabilis*, loc. cit., p. 243.

pentagonal, while in others there is a smaller number of actinal plates than usual, but *Palæostoma* is the only genus in which a regular radiate arrangement is perceptible. The actinal membrane of all *Desmosticha*, whether it be regularly imbricated or not, bears ten large prominent interradial plates, which are pierced by the ten large buccal tentacles.[1] They appear to develop from the continuous plating of limestone cells which extends over from the abactinal side so as to cover the whole actinal surface of the young Urchin. They are found in all young *Echini*, being the first plates to appear of all those on the actinal membrane,[2] while in many genera they always retain a "greater preponderance." Agassiz[3] regards them as homologous with the five actinal plates of *Leskia*, and they would therefore represent the five oral plates of the Crinoids. This view is strengthened by the fact that they are pierced by the ten large buccal tentacles, much in the same way as the ocular plates (=radials) are said to be pierced by the odd terminal tentacles of the ambulacra, while the orals of the young Crinoid are also opposite to five pairs of short tubular tentacles placed interradially, though not perforated by them. These orals alternate with five large azygos tentacles, the homologues of which in the Urchins separate each pair of buccal shields, and ultimately become the odd terminal tentacles.

I am by no means sure that Agassiz is right in comparing these buccal plates of the *Desmosticha* to the oral valves of *Leskia*. In the first place they are paired and perforate, while the latter are single and imperforate. This, however, is a comparatively unimportant difference. The one on which I would lay most stress is the mode of origin of the buccal shields, which is very different from that of the oral plates of Crinoids. Agassiz himself describes them as formed by an extension of the limestone plating from the abactinal over on to the actinal surface. It can, of course, be urged that this be also the origin of the oral valves of *Leskia*. If so, they cannot be homologous with the oral plates of the Crinoids; but, as far as mere appearance goes, they resemble these far more than they do the ten perforate buccal shields of the *Desmosticha*. Lovèn,[4] however, gives an entirely different interpretation of these buccal shields.

[1] 'Revision of the Echini,' p. 699, plates ix, figs. 2 and 4, and x, fig. 3.
[2] 'Revision,' p. 735.
[3] 'Revision,' p. 583.
[4] Loc. cit., pp. 27—29.

He regards them as the "rudiments of the first primary plates of the ambulacra," which are arrested in their extension towards the peristome by the resistance of the auricles that are attached to the internal surfaces of the ambulacral plates, and serve as supports to the lantern. For between every two pairs of these, nearer the periphery, he finds smaller triangular plates intercalated, which he regards as the first traces of the interradial areas. In the *Cidaridæ*, however, the bases of the auricles are interradial, and they therefore offer no resistance to an extension of the ambulacra towards the margin of the corona. As the plates successively reach this margin, their sutures are opened and they undergo considerable changes, so as to give rise to the imbricated plates of the actinal membrane, which are therefore merely metamorphosed ambulacral plates. In many Urchins (*Echinus, Temnechinus, Strongylocentrotus*) the actinal membrane is quite bare, with the exception of the ten perforated buccal shields. These are formed very early near the edge of the test, but gradually approach the bases of the teeth during development. In certain genera (*Porocidaris*) small imbricating plates are formed between them and the teeth, while the remaining peripheral part of the membrane is left bare. More commonly, however, this is covered by imbricating plates in greater or smaller number. Thus, in *Hemipedina* the ten buccal plates are large and occupy nearly the whole membrane, which bears eight or ten very much smaller ones between them and the test. But in *Salenia* and *Toxopneustes* the membrane is chiefly covered by a number of imbricating plates closely packed together, though the ten perforated buccal plates remain distinct. In *Trigonocidaris* they are but slightly more prominent than the others, and in the *Diadematidæ* and *Cidaridæ* all trace of them is lost, at any rate in the adult, as seems also to be the case among the irregular Urchins. In *Echinothrix* and in the *Echinothuridæ* the actinal membrane is covered, as in the *Cidaridæ*, by a number of movable imbricating plates, which perform the part of ambulacral and interambulacral plates, like those of the test of an ordinary Urchin. For the imbricated plates continuing the ambulacral system on to the actinal membrane are pierced for suckers identical with those of the rest of the ambulacral zone, extending unbroken to the actinostome as far as the buccal tentacles, which are not different in size from the other ambulacral tentacles.

These imbricating buccal plates which Lovèn regards merely as metamorphosed ambulacral plates, form a much

larger proportion of the test of the *Cidaridæ* than the plates on the actinal membrane do in the other Urchins. For the number of coronal plates is small, especially in young specimens, the test of which seems to consist almost entirely of an actinal and abactinal system, separated by a narrow band of coronal plates. Further, these imbricated buccal plates are arranged radially in rows made up of more than two plates, with the plates lapping in opposite directions in the ambulacra and interambulacra. These peculiarities are also found in the plates not only of the buccal membrane, but also of the corona of the *Echinothuridæ*, and they are characteristic of the *Palæchinidæ*. Hence, Agassiz[1] has suggested that the test of these last was made up of plates homologous with the buccal plates of *Cidaris*. Were the narrow band of coronal plates in a young *Cidaris* to disappear entirely, and the buccal plates to take a correspondingly great development, we should have a spherical Urchin agreeing in every respect with the typical *Palæchinus*. The test would be reduced to the actinal and abactinal systems, and be entirely made up of small ambulacral and interambulacral plates consisting of several rows, and homologous with those of *Asthenosoma* and *Cidaris*. Instead of regarding the test of a *Palæchinus* as consisting only of an abactinal, together with an enlarged actinal system, Agassiz[2] has pointed out that the latter may be also considered as a corona, reaching almost to the jaws, the actinal membrane being reduced to an insignificant member, as in the Clypeastroids. This view is essentially similar to that put forward by Lovèn. It appears to me that it is the more correct of the two, and I imagine that the *Palæchinidæ* exhibit to us a condition of the Echinoderm skeleton, closely similar to, and yet different from that which is found in many Crinoids.

It is worth notice that there are many Holothurians, the condition of which is in some measure comparable to that of the *Palæchinidæ* and *Echinothuridæ*. Thus, in *Psolus*, *Ocnus*, *Colochirus*, and *Echinocucumis*, there is a flexible test, i. e. a thick leathery membrane, in which large calcareous plates are imbedded, and in *Colochirus* they are pierced for the tubular feet. The homology of these plates with the test of *Echini* has been already pointed out by Semper.[3] In *Psolus* there is also an oral system, but no distinct apical system has been traced, while in the *Perisso*

1 "Revision," pp. 257, 646.
2 "Revision," p. 646.
3 "Reisen im Archipel der Philippinen," ii, 1. 'Holothurien,' p. 58.

echinids the reverse is the case. In the irregularity of the plating the Holothurians resemble the Crinoids, but even in the latter there are traces of a radiate arrangement in the plating of the disc, which resembles the alternation of the ambulacra and interambulacra in the test of an Urchin. Thus, in *Pentacrinus*,[1] there are rows of small marginal plates at the sides of the ambulacra, and in the interradial and interbrachial areas between them are the perforated anambulacral plates. These marginal plates at the sides of the ambulacra also occur on the disc and arms of *Rhizocrinus*, and on the arms of *Pentacrinus*, *Hyocrinus*, *Bathycrinus*, and of the young *Antedon*, in which they ultimately undergo resorption. Wachsmuth[2] has found them also in the arms of *Cyathocrinus* and of other Palæozoic Crinoids, in which they are borne upon small quadrangular plates situated on the outside of each groove, and interlock with one another over the middle line of the groove so as apparently to close it completely. Wachsmuth believes that they were movable, and only closed over the furrow when the arms were folded up. Müller found an outer row of plates supporting the delicate marginal plates of the ambulacra of *Pentacrinus* of the same nature as those described by Wachsmuth in *Cyathocrinus*, and he seems to have called them *adambulacral* (fig. XIV, *ad*), and to have regarded them as homologous with the similarly named plates in the Asterids and Ophiurids.[3] In this I entirely concur, and I would go still further and compare the double row of marginal plates covering the ambulacral grooves (fig. XIV, *sup.*) to the ordinary *superambulacral* plates in the test of the Urchins, and in the *Ophiurids*.

In most Ophiurids these plates are arranged in a single row, but they are primitively double, as in the young Asterids, in which they ultimately become resorbed. In the Urchins this is not the case, and the ambulacral areas consist of two rows of plates, but they differ from the marginal plates of *Pentacrinus* and most other *Crinoids* in being perforated by pores, through which the tubular feet reach the exterior. In *Cyathocrinus*, however, Wachsmuth has found the apices of these marginal plates to be perforated, so that the course of the ambulacra is marked out by double rows of small pores, very much as in the Urchins.

Another striking resemblance between the elements of the

[1] Müller, "*Pentacrinus*," loc. cit., p. 49.
[2] Loc. cit., pp. 120—124.
[3] See Huxley's "Lectures on General Natural History," 'Medical Times and Gazette,' Dec. 13, 1856, p. 587.

ambulacral skeleton of the Crinoids and of the other Echinoderms has already been mentioned. Underlying the ambulacra on the disc of *Pentacrinus*, Müller[1] found a series of median azygos plates, which he termed *subambulacral*, and he compared them to similar plates found by Roemer beneath the ambulacra of the Blastoids. I pointed out above that they are also represented in the Palæocrinoidea. Müller rightly regarded them as corresponding in their position with respect to the water vessel with the radial ossicles of the oral calcareous ring in the Holothurians, and with the rotulæ in the lantern of *Echini*. Simroth[2] has shown that there are good reasons for regarding the rotulæ (together with the radii) and the auricles as respectively representing the first and second vertebral ossicles of the Starfish arms. Had Müller continued to hold his original views, which are now generally accepted, as to the homology of the radial pieces of the oral ring in the Holothurians with the auricles of the *Echini*, and with the vertebræ of the Starfish arms, he would, no doubt, have also described these last as subambulacral.[3] The principal component of the Crinoid skeleton being anti-ambulacral (or abactinal) is, of course, not to be found in the Urchins, and is only imperfectly represented in the Starfishes.

It is merely an extensive development in a radial direction of the primitive abactinal or apical system, situated at the dorsal pole of the larva, which is of extreme importance in Echinoderm morphology, for, as shown by Agassiz,[4] it is the foundation of the whole skeleton, whether anti-, sub-, or super-ambulacral. "In fact, the external limestone plates forming the test of a Sea-urchin, the reticulated network of the actinal and abactinal surface of a Starfish, together with the ambulacral and interambulacral plates and the plates forming the disc of an Ophiuran, the upper, lower, and side arm-plates, as well as internal skeleton, are all directly derived from the simple system of limestone plates of the abactinal surface of the Echinoderm embryo."

In the Crinoids the abactinal or antiambulacral system remains most nearly in its primitive condition, extending but very slightly towards the actinal side. But in the other Echinoderms the radial plates of the abactinal system, situated round the dorsal pole of the embryo, gradually extend towards the edge of and down on to the actinal side, so

[1] *Pentacrinus*, loc. cit., p. 49, and 'Bau der Echinodermen,' pp. 57, 58.
[2] "Anatomie und Schizogonie der *Ophiactis Virens*," Sars., Zweiter Theil, 'Zeitschr. für Wiss. Zool.,' xxviii, pp. 511, 512.
[3] See Addenda, No. 6, p. 205.
[4] 'North American Starfishes,' pp. 91—93.

as to enclose the water-system. The Ophiurids and Urchins remain permanently in this condition, but in the Asterids the superambulacral plating is resorbed along the central line, its edges sending out small spurs to form the vertebral ossicles or subambulacral system, which makes up the principal element in the Starfish skeleton. In the Crinoids, however, no extensive changes of this kind take place, and in this respect, as well as in the condition of their actinal skeleton, they are in a far more embryonic condition than are the other Echinoderms, so that we have another strong piece of evidence in favour of the view that they are phylogenetically the oldest members of the group.

It will have been gathered from the foregoing pages that the general views which I hold respecting Echinoderm morphology are essentially those of Johannes Müller, as modified and extended by A. Agassiz. Götte,[1] however, has recently put forward some considerations which have led him to adopt precisely the opposite of Müller's views, namely, that the apex of a Starfish represents the whole convex part of an Echinid shell, instead of the apex of the Urchin corresponding to the whole antiambulacral surface of the Starfish. Further, Götte considers the arms of the Crinoids to be homologous with the oral tentacles of the Holothurians. A view similar to this was put forward some time ago by Wyville Thomson,[2] and also later by Huxley,[3] who seems to have subsequently abandoned it, as there is no mention of it in his 'Anatomy of the Invertebrata.'

Götte regards the Echinoderm skeleton as, so to speak, the result of a combination in varying degrees of two modes of radiation which are essentially opposed to one another. One of these systems corresponds in position with the water-vascular trunks, and is thus *radial* as regards the general symmetry of the Echinoderm type. In the brachiate orders (Starfishes and Crinoids) it forms the skeleton of the arm bases. The other skeletal system, as seen in the Crinoid, is that of the first formed part of the calyx, viz. the basis, on the abactinal surface of the body, together with the oral system of the actinal surface. This system alternates in position with the tentacle-bearing arm bases, and is, therefore, interradial. It is the more prominent of the two in the young *Comatula*, in which the basals and orals attain a considerable size before the appearance of the radials.

[1] Loc. cit.,' pp. 627—630.

[2] 'Edinburgh New Phil. Journal,' loc. cit., p. 115.

[3] "Notes on the Invertebrata," 'Medical Times and Gazette,' Aug. 14, 1875, pp. 173, 174.

Later on, however, they undergo a considerable regressive metamorphosis, while the abactinal skeleton of the arms develops very rapidly, as the water-vascular stems extend outwards from the disc, bearing with them the odd terminal tentacle. This mode of growth, with some slight modifications, is common to the Asterids and Ophiurids, the arms of which, as of the Crinoids, may be regarded as an extreme development of the primary tentacular cæca borne upon the water-vascular ring of the larva, which becomes much enlarged and acquires a calcareous skeleton. The water-vascular ring of the Holothurian embryo also bears five tentacular cæca, but the water-vascular trunks indicating the five antimera, are not formed (when present) by these cæca being carried outwards away from the ring, as is the case in the Starfishes; for they appear separately as five other diverticula from the water-vascular ring, alternating with the tentacular rudiments.

Götte assumes that these cæca are of primary importance, and occupy a similar position in all Echinoderms. He is consequently led to regard the Starfish arms, with their primitive terminal tentacles, as homologous with the branching tentacles of the Holothurians. In the same way he compares the intertentacular antimers of the Holothurians to the interradial antimers of the Crinoids; for these which contain the basal and oral plates, alternate with the tentacle-bearing arm rudiments, that ultimately attain so great a development and obliterate or obscure the primary interradial skeleton.

I regret that I am unable to accept Götte's views. He brings forward no argument in their favour, except, of course, one of time, namely, that the five cæca which first appear as outgrowths of the water-vascular ring, develop in the Holothurians into the branched oral tentacles, and in the Starfishes into the large terminal tentacles at the ends of the arms. Further, if Gotte's views are correct, the conclusions which naturally follow from them are completely at variance with many facts of Echinoderm morphology. He regards the condition of the *Echini* as essentially similar to that of the Holothurians, though the ambulacral areas are not completely homologous in the two groups, owing to the presence of interambulacra in the Urchins, and to slight differences in the mode of origin of the water-vascular trunks. In the Urchins the "ursprünglichen Tentakelanlagen werden nicht in Arme fortgesetzt, deren Entwickelung eine besondere aborale Strahlgliederung unterdrückte und die damit alternirende orale Gliederung zur ausschliesslich herrschen-

den machte ; indem also Fortsetzungen der ersten Tentakelgefässe in den aboralen Körpertheil hineinwachsen, bezeichnen die von ihnen gebildeten Ambulacralfelder nicht die einzigen Strahlsegmente, sondern wechseln regelmässig mit den Interambulacralfeldern ab, welche gewissermassen ein Strahlsystem für sich bilden, da auch ihre ersten Skeletanlagen gleichzeitig mit den ambulacralen aber unabhängig von denselben und nicht paarig gerade so wie die radiären Rückenplatten der Seesterne entstehen."

I must confess that I cannot agree with these conclusions of Götte's. On his own showing, the water-vascular stems in the embryo Urchin do not alternate with the primary tentacular cæca as in the Holothurians, and yet the antimera they indicate are supposed by him to be homologous in the two cases. If the relative positions of the primary tentacular cæca and of the water-vascular stems are morphologically as important as Gotte supposes, surely he is somewhat inconsistent in completely disregarding them, as in the case just quoted. Krohn[1] states that the five primary tentacles of the young Urchin disappear, instead of persisting and branching as in the Holothurians; but according to Agassiz[2] and Lovèn[3] the mode of growth of the new tentacles is the same as in the Starfishes. They are formed in successive pairs at the bases of the large primary tentacles, which are thus carried away from the water vascular ring as the test enlarges and the radial stems elongate. Agassiz[4] states positively that they pierce the ocular plates, but Perrier[5] altogether denies this. Whether they are present in the adult or not, the fact that they terminate the growing water-vascular trunks, as in the Starfishes, is a sufficient argument against Götte's views, which are based upon the hypothesis that the arms of the Starfishes are not homologous with the ambulacral areas of the Urchins and Holothurians, but with the buccal tentacles of the latter. Upon this hypothesis the ambulacra of the Urchins are supposed to be developed altogether from the right antimer, like the apex of the Starfishes and the basis of the Crinoids. Götte therefore regards the aboral portions of the Starfish body as equivalent, not merely to the apex, but to the whole convex portion of the Echinid shell, the ventral side of which

[1] Müller's 'Archiv,' 1851, p. 351.
[2] 'Revision,' p. 725.
[3] 'Loc. cit., p. 28.
[4] 'Revision,' p. 682.
[5] "Recherches sur l'Appareil Circulatoire des Oursins," 'Archives de Zoologie Expérimentale et Générale,' vol. iv, p. 622.

represents the peristomial area of the Starfish; while the arms of the latter are structures peculiar to it, and therefore not comparable to any parts of an Urchin. This is of course a complete reversal of Müller's idea that the apex of the Urchins represents the whole antiambulacral dorsum of the Starfish. So far as the actual origin of the ambulacral plates is concerned, there is some ground for this hypothesis of Götte's; for Agassiz has shown that the external limestone plates forming the test of a Sea-urchin are all directly derived from the simple system of limestone plates on the abactinal surface of the embryo. But he has also shown that the reticulated network of the actinal and abactinal surface of a Starfish, together with the ambulacral and interambulacral plates, have the same origin, which tells strongly against the truth of Götte's hypothesis.

Other considerations too, demonstrate the general correctness of Müller's views. The corona of the Urchins is the result of an extreme vertical elongation of that portion of the equatorial zone of the larva that lies between the peristome and the radials (=oculars), which last remain in close contact with the basals (=genitals). It may, therefore, be termed *extra-radial*. In the Crinoids the radials also remain in close proximity to the basals, as in the Urchins, but the equatorial zone is very much extended horizontally. It is supported by a dorsal skeleton, which is built up gradually upon the radial circlet, and is also therefore extra-radial, or better, *supra-radial*. In the Starfishes, on the other hand, there is a similar lateral extension of the equatorial zone which forms the ventral surface of the arms, but their dorsal surface is altogether unrepresented in the other Echinoderms, and may be called *intra-radial*. For it is the result of a separation of the radials from the rest of the calyx by a constant formation of new spines at the base of each ray, so that instead of their resting directly on the basals there is a long interval between the two rings of plates. The dorsal surface of a Starfish is therefore strictly comparable to the apex of an Urchin or the calyx of a Crinoid (as far as the first radials), as was supposed by Müller. But between the arms of a Starfish or Crinoid and the ambulacra of an Urchin, there is only a general homology, not one which can be followed in much detail.[1]

The views advanced above may perhaps be better understood by the help of the accompanying simple diagrams. If the basal, radial, and oral circlets of the young Crinoid be

[1] Compare Agassiz, 'Revision,' pp. 758—760, and 'North American Starfishes,' pp. 87, 88.

represented by the letters B, R, and O respectively, their relative positions just after the appearance of the radials are represented in fig. 15. The line separating RR and O indicates the position of the above-mentioned equatorial zone separating the oral system developed around the left peritoneal sac, from the calyx which is formed around that of the

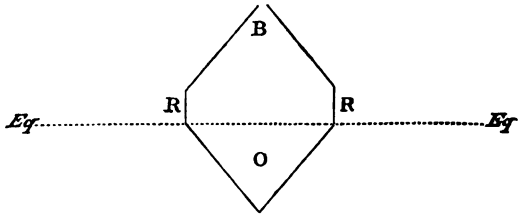


FIG. XV.—Diagram showing the relative positions of the basals, orals, and radials, in an early stage of the development of a Crinoid. B. Basal. O. Oral. R. Radial. *Eq.* Line indicating the position of the equatorial zone which separates the oral and apical systems.

right side (compare figs. I, VIII, IX in Part I). Fig. XVI shows the mode in which the supra-radial antiambulacral skeleton

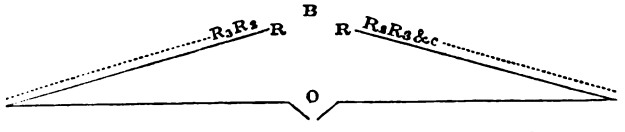


FIG. XVI.—Diagram showing the relations of the apical and oral systems in an adult Crinoid. B O R. as in Fig. XV. R_2 R_3. Second and third radials.

of the arms of a Crinoid is formed in support of a lateral extension of the equatorial zone. In the Urchins and Holo-

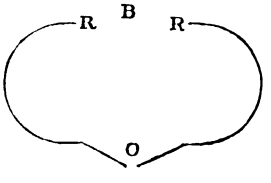


FIG. XVII.—Diagram showing the relative positions of the basals, orals, and radials in *Leskia mirabilis*. Lettering as in Fig. XV.

thurians, however, the extension of the equatorial zone is in a vertical direction (fig. XVII), and in the former it becomes covered by a superambulacral plating, which extends over on to it from the abactinal side.

In the Starfishes (fig. XVIII) the radials are carried out from

the calyx by the constant formation of new spines at the base of each ray, which are supported by a long narrow limestone plate, extending distinctly from the basal plate almost to the terminal radial. This plate, according to Agassiz, is also derived from the primitive abactinal system, as are the superambulacral plate on the actinal surface with the subambulacral spurs formed from its edges. It is comparable to the antiambulacral arm skeleton of a Crinoid, except that it is *intra-* instead of *extra-radial*. The super-

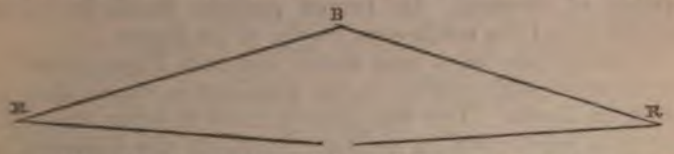


FIG. XVIII.—Showing how the radials R of the young Starfish are carried away from the basals (= genitals) B, and form the ocular plates at the ends of the arms.

ambulacral plate is absorbed in the Asterids, but persists in the Ophiurids as the ventral plating of the arm. The plating of the grooves on the ventral surface of the Crinoids, although occupying a superambulacral position, does not seem to have the same origin as the corresponding plating in the Starfishes. The precise homologies of the ambulacral grooves of the Crinoids in the other Echinoderms have yet to be worked out, but I am inclined to think that Greeff's suggestions[1] are right in their general principle. Agassiz's observations support them as far as the Urchins and Starfishes are concerned, while those of Götte, on the other hand, demonstrate that the ambulacral grooves of the Crinoids are a peripheral extension of the tentacular vestibule of the larva, the floor of which forms the peristomial area whence the groove-trunks radiate. This vestibule (fig. XIII, *lp'*) is derived from the left or oral division of the enterocœl, so that the ambulacral epithelium (fig. XIII, *ae*) covering its floor and the so-called "ambulacral nerve" beneath it must be hypoblastic in their origin. Further, in many *Actinometra* these structures are altogether absent from several of the posterior arms, as if the growing vestibule had been unable to extend itself so far from the oral ring, which in this genus is excentric or even marginal.

We have yet to learn that the ambulacral or nerve-epithelium of the other Echinoderms is a hypoblastic organ, and that the grooves of the Starfish arms are derivatives of the

[1] "Ueber den Bau der Echinodermen," 'Dritte Mittheilung. Marburg Sitzungsberichte,' No. 11, 1872, pp. 165—169.

cannot but result in a dire confusion of terms. Thus, the subambulacral plates of the Ophiurids would represent the superambulacral ones of the Crinoids and Urchins, and *vice versâ!* On page 267 Ludwig takes Simroth to task in the following words for doing very much the same that he has done himself—"Verwirrung aber wird durch Simroth dadurch angerichtet, dass er die für diese Skeletstücke von Joh. Müller eingeführte Bezeichnung auf andere Stücke überträgt." Substitute my friend Ludwig's name for Simroth's in the above sentence, and his own words become applicable to himself!

The DEVELOPMENT *of the* EARTH-WORM, LUMBRICUS TRAPEZOIDES, DUGÈS. By NIKOLAS KLEINENBERG. (With Plates IX, X, XI.)

IN Ischia, as in the neighbourhood of Naples, the most common of the Lumbricidæ is *Lumbricus trapezoides* (Dugès); it is abundant in gardens and in the muck-heaps of farms. Associated with this, but rarer, and prefering sandy soil and the neighbourhood of water, is another species, probably *Lumbricus teres* (Dugès).

The reproduction of *Lumbricus trapezoides*, like that of *L. teres*, is most active during the whole of the cold and temperate season, that is to say, from October to June, when the hot and dry weather begins, but never ceases altogether, since even in July and August capsules containing fecundated eggs are found in shady and damp places, and at a considerable depth; many of these, however, perish.

The capsules vary greatly in size; the smallest are hardly one millimètre, whilst the largest reach eight millimètres in length. This difference is easily explained by the mode of formation of the capsules, since necessarily their dimensions must correspond to the size of the animal producing them. The shape of the capsules of *L. trapezoides* is oval, with the ends pointed, or sometimes, on the contrary, slightly depressed; such depressions correspond to the primitive opening of the chitinous ring formed by the clitellus, which does not close till after deposition.

Their colour resembles that of corn. The capsules of *L. teres* are in general smaller, more resembling a lemon in shape, often with the ends greatly elongated to form two fine processes. These capsules are olive-coloured.

The contents of the capsules of *L. trapezoides* consist of an albuminous mass, in which, as Rathke has demonstrated in *Nephelis vulgaris*,[1] two constituents are distinguishable, namely, a dense, transparent, strongly refracting substance, forming a kind of sponge, with very fine interstices, and a liquid which fills these interstices. The albumen, under the action of water, of acids, or of alcohol, assumes the appearance of an emulsion, in consequence of the precipitation of very fine granules, a decomposition which occurs during the progress of development in capsules which have been left intact.

The albumen of the capsules of *L. teres* is colourless or faintly tinged with greenish, is much more dense, and of a nearly uniform aspect; it does not *dissolve*, except very slightly, in water or in dilute acids.

In this jelly the eggs are scattered, and between them bundles of spermatozoa. The number of the eggs in the capsules of *L. trapezoides* is from three to eight, in those of *L. teres*, it is from four to twenty, all of which become fecundated and develop; on the other hand, in the capsules of *L. trapezoides* one egg only, or rarely, two or three, produce embryos. The other eggs not undergoing the exciting influence of the male element, lose their spherical form and become transformed into flat plates, with more or less irregular outlines; the protoplasm, by a kind of coagulation, changes into a dark substance, containing large granules, and the eggs gradually dissolve and vanish without leaving a trace.

Methods of Investigation.

I should have undertaken the study of the development of *L. teres* more willingly than that of *L. trapezoides*, since in the former the first stages are more simple and typical, and even the later stages clearer and more distinct. Accidental conditions, however, render the preparation extremely difficult. The density and viscosity of the albumen, together with the excessive delicacy and fragility of the embryos, make it very difficult to obtain any of them uninjured. Further, as they rapidly devour the whole of the albumen and store it up in the digestive cavity, their body-walls becomes so tense that the slightest pressure is enough to bust them. For these reasons my knowledge of the development of this species remains incomplete, and I shall limit myself at present to the description of the development of *L. tra-*

[1] Rathke, Beiträge zur Entwicklungsgeschichte der Hirudineen. Herausgegeben, von R. Leuckart. Leipzig, 1868, p. 3.

pezoides, whose embryos may be readily extracted from the albumen without injury.

A great part of the earliest formations of the egg can be made out in the living state, the protoplasm being sufficiently transparent to allow the internal parts to be seen; but afterwards the precise outlines of the cells disappear, and nothing can be seen but the grosser structure. To make out the more delicate structure it is necessary to employ reagents.

Of these I have employed several: osmic acid applied in the state of vapour gives good results; but the preparations obtained by the use of a mixture of picric with sulphuric acid were more satisfactory. This reagent, however, has the same drawback as osmic acid, namely, that of occasionally producing swellings in the primitive blastomeres, a circumstance which, if it only slightly alters the normal conditions, renders the preparations less sightly. This difficulty is overcome by the addition of a little kreosote.

As I am now able, after many experiments, to recommend strongly the method of preservation which I have here used, and for the majority of other animal tissues, especially for the more delicate and perishable, I think it may be useful to give the exact receipt.

Prepare a saturated solution of picric acid in distilled water, and to a hundred volumes of this add two volumes of concentrated sulphuric acid; all the picric acid which is precipitated must be removed by filtration. One volume of the liquid obtained in this manner is to be diluted with three volumes of water, and, finally, as much pure kreosote must be added as will mix.

The object to be preserved should remain in this liquid for three, four, or more hours; then it should be transferred, in order to harden it and remove the acid, into 70 per cent. alcohol, where it is to remain five or six hours. From this it is to be removed into 90 per cent. alcohol, which is to be changed until the yellow tint has either disappeared or greatly diminished. Alcohol of 90 per cent. is better than absolute for preserving the more delicate structures for a long time uninjured, and for keeping the preparation at the proper degree of hardness.

For colouring I use crystallised hæmatoxylin dissolved in the following mixture:—Prepare a saturated solution of calcium chloride in 70 per cent. alcohol, with the addition of a little alum; after having filtered, mix a volume of this with from six to eight volumes of 70 per cent. alcohol. At the time of using the liquid pour into it as many drops of a concentrated solution of hæmatoxylin in absolute alcohol as

are sufficient to give the required colour to the preparation of greater or less intensity, according to desire.

This mixture, notwithstanding its chemical irrationality, gives good results. Aqueous solutions, especially when they contain traces of ammonia, are to be avoided, since they are very hurtful to many delicate tissues. The object must remain in the dye for a period varying from a few minutes to six hours, according to its size and to the nature of the tissues composing it. It is a good rule, when intending to make sections, to stain deeply and to cut *them very thin*.

When removed from the dye the preparation is to be washed in 90 per cent. alcohol, in which it may remain from six to twelve hours. Finally, to remove every trace of water, it should remain for half or a whole day in absolute alcohol.

If the preparation is to be cut it must be removed from absolute alcohol to essential oil of bergamot, in which it should remain for some hours, in order to fit it for being embedded in paraffin, which is removed from the sections when cut by means of a mixture of four parts of essence of turpentine with one part of kreosote. Finally, the sections are mounted in resin dissolved in essence of turpentine.[1]

I have made sections from the beginning of segmentation, but in the earliest stages these have not been of very much use, since it is impossible to place such small globular bodies in a determined position; the direction of the sections is either not that required or is altogether uncertain. In consequence I preferred studying the beginning of the development by means of optical sections of the entire object, always, however, using real sections to control the results.

Segmentation of the Egg and first appearance of the Embryos.

I have failed to observe the phenomena in the fecundated egg immediately following the fusion of the sexual elements. The earliest eggs which I have observed were already divided by an equatorial furrow into two embryoplastic segments or blastomeres. In this stage the egg is still contained in the vitelline membrane, which is an oval capsule of about 0·24 mm. in length, whose very thin walls are without any trace of structure. Its contents consist of a limpid, colourless fluid,

[1] Histologists are warned not to use a solution of resin in alcohol. The preparations mounted in this are at first beautiful but soon become spoiled, in consequence of the precipitation of crystals or of an amorphous substance. I have lost in this manner many hundreds of preparations, and the same results have occurred in the Zoological Station at Naples.

slightly refractive, and holding in suspension the egg, and near it two or three polar globules—protoplasmic corpuscles containing one or more large vacuoles. The egg itself is an ellipsoidal body, whose normal axes measure about 0·14 and 0·10 mm. Its protoplasm is without vitelline corpuscles, and is therefore pale and transparent; it is divided, as in so many other eggs, into two substances: one, more compact and with fine granules, is disposed in a network, or rather in the form of a sponge, with relatively large spaces; the other is a clear, uniform, albuminous liquid, which fills the spaces. On the surface the protoplasm is somewhat condensed, so as to form a very thin cortical stratum.

The two hemispherical blastomeres sometimes fit themselves with their plane surfaces so perfectly in contact that it is impossible to separate them. Sometimes the centres of the planes of contact become slightly excavated, and so separate, leaving between them a central lentiform space, while the margins still remain firmly adherent. This space might be called the beginning of the segmentation cavity, if the changes in form of the blastomeres did not soon make it disappear. In fact, after a short period of rest, a tendency arises in each blastomere to assume the spherical form, by which the peripheres of their respective bases are drawn towards the corresponding centres, and becoming curved separate from one another, so that finally they touch only at a single point, in the place where the lentiform cavity formerly existed.

The first two blastomeres at one time show distinct nuclei; at another are deprived of them; at another show with great clearness those stellate or radiating or fusiform groups of fine granules, which the beautiful researches of the last few years have shown to be phenomena constantly accompanying the formation of new cells.

The process of segmentation of the eggs of *L. trapezoides* does not proceed in so simple and orderly a way as in many other animals, and in not a few of the Annelids; soon begins a series of alterations in shape and position, of divisions and buddings, of increasings and diminishings of volume of the single cells, which altogether make it very difficult to trace the type of this most important process, which, as the first manifestation of the formative forces hidden under the apparent sameness of the protoplasm, serves as a beginning for the building up of the complicated and definitely disposed structure of the body.

After the division into two hemispheres a stage is often observed in which the egg is composed of three blastomeres, arranged in the form of a triangle, already described by

Kowalewsky,[1] by Ratzel and Warschawski[2] in *Lumbricus agricola*, by Rathke[3] and Robin in *Nephelis vulgaris* (in which I have also observed it), and by Claparède and Metschnikow[4] in *Spio fuliginosus*; this last observation I am also able to confirm from my own investigations. Such a stage of segmentation, though different enough from what is usually found in other animals, certainly cannot be considered abnormal as in so many other cases, in which irregularities of segmentation are the first and certain sign that the egg is under unfavorable conditions and is about to break up before having attained any considerable development; it appears, on the contrary, certain that in these worms this phase, though departing from the general rule, leads on to a healthy development. But the division into three blastomeres does not occur in all the eggs of *L. trapezoides*, and is not indispensable to the regular progress of development. Sometimes it happens that the first two blastomeres each produces at the same time a new cell, so that four immediately succeed two. The process of segmentation then proceeds in the following peculiar manner:—In the midst of the protoplasm an accumulation of fine granules appears, which is easily distinguished as a dark spot; this aggregation of the more solid parts of the protoplasm, which, however, has not distinct limits, increases gradually in size and at the same time approaches the surface of the segment. It is advisable to state that this concentration is not to be confounded with the phenomena which prepare and accompany the first formation of nuclei; the nucleus appears later in the centre of the mass described above. The mass, as soon as it has arrived at the surface, raises itself above the level of the surrounding protoplasm in the form of a slightly projecting cone; then, by a narrowing of its base, it separates from the mother-cell and a new blastomere is formed.

This observation agrees in nearly all particulars with that of Kowalewsky on the formation of the small segments in the egg of *Euaxes*.[5]

The two blastomeres of the second generation remain very much smaller than the first; at first situated symmetrically with regard to the long axis of the egg, they then approach one another, advancing towards the median line, and at the same

[1] "Embryologische Studien an Würmern und Arthropoden," 'Mém. Acad., St. Petersbourg,' 1871. Tab. vi, fig. 3.
[2] 'Zeit. für Wiss. Zool.,' T. 18, 1868.
[3] Loc. cit., Tab. i, fig. 6.
[4] "Beiträge zur Kentniss der Entwicklungsgeschichte der Chætopoden," 'Zeit. für Wiss. Zool.,' 1869, T. 19, Tab. xii, fig. 1, d.
[5] Loc. cit., pp. 13, 14.

time two other small cells separate themselves from the first blastomeres; the egg consists of six segments, two large and four small. A short time later two more cells are added to the last, and in this manner a little plate of small *flattened* cells is formed, which, resting upon the top of the two large blastomeres, covers like a roof the gradually widening furrow which separates them (Pl. IX, fig. 1.)

Such a stage of segmentation is much like one already described in the development of *Nephelis*, with the difference, however, that this, instead of two, possesses three large cells, covered in part by a layer of smaller cells. But there is a still more important difference: while in *Nephelis* the large blastomeres remain for a long time unaltered, those of *Lumbricus* soon divide repeatedly, and become blended with the general embryonic mass. At first they separate from one another, leaving in the middle a wide and deep space, one side of which is closed by the curved plate of small cells, whilst the other presents a somewhat restricted aperture opening into the cavity of the capsule. Now the two large blastomeres each divide contemporaneously into two, and at the same time some of the small blastomeres tend towards the centre, interposing themselves between the four large ones. After repeated divisions, which influence the large as well as the small blastomeres, the egg assumes a very characteristic appearance; there are in all sixteen blastomeres, and if sometimes there is one more or less it is always one of the small ones.

Of the six large blastomeres three are grouped round the aperture of the segmentation cavity, which they have closed or reduced to a narrow slit; above and alternating with these are the three others, but these do not touch each other, being separated by means of three small blastomeres, which are placed like wedges between them. The ring thus formed of three large and three small blastomeres embraces the segmentation cavity, and is covered above by a thin roof composed of five or six small blastomeres. Unfortunately such clear arrangements are of too short duration in the first days of development of the animal under consideration. Very soon it comes to pass that by the multiplication, as well of the large as of the small blastomeres, the differences in size between them presently disappear, and, further, the introduction of the small blastomeres between the offspring of the large ones, contributes to the destruction of the above-mentioned order.

For a time some of the first blastomeres remain upon the surface external to the others, but when these also are dis-

placed towards the centre we have a new form of the egg, which no longer shows any trace of the arrangement which preceded it. It is now a little spherical bladder, sometimes, as far as can be seen, perfectly closed; sometimes furnished with a small opening, whose walls consist of a single layer of cells, which vary considerably in length. About one pole the cells are longer than they are broad, while at the opposite pole the wall of the segmentation cavity is composed of a series of cells, whose length is half that of the others or less. There is not, however, a distinct boundary between these two kinds of cells; they rather pass the one into the other by numerous gradations. There is not even a difference in the protoplasm; in all it is uniform and finely granular, since the reticular arrangement of the protoplasm of the egg and primary blastomeres has already disappeared some time; each cell now nearly always contains a very distinct nucleus, whose volume varies with that of the cell. The egg in this manner is transformed into a germinal bladder, consisting of a single layer of cells of different length, surrounding a somewhat large eccentric cavity, which opens—if not always, certainly in some cases—by a narrow opening (Pl. IX, fig. 2).

After this the reproductive activity is most marked in the flat cells at one pole of the egg; they increase in number, become longer and push into the segmentation cavity, pushing through its aperture or making their way between the neighbouring loosely connected cells. But at the other pole small cells detach themselves from the central extremities of the long blastomeres; in this manner the segmentation cavity, restricted on all sides, disappears, and the egg becomes a solid and compact multicellular sphere.

I shall, perhaps, have wearied the reader with the minute description of the succession of changes, which, nevertheless still remains somewhat nnintelligible in consequence of the scarcity of illustrations. But the importance of the argument and the divergence existing between my results and those of such an excellent observer as Kowalewsky, must be my excuse for the detailed nature of the account I have given. According to the author above cited, the first phases of development in *L. agricola* are very simple and regular. The segmentation produces almost from the first cells of of equal size, and a disc-shaped body is formed, which becomes divided by a fissure, representing the segmentation cavity, into two laminæ, each consisting of a single layer of cells; these soon become distinguishable by the nature of their protoplasm. The circumference then raising itself

above the lamina of clear cells, the disc assumes the form of a cup, which by the narrowing of its mouth becomes gradually a typical blastodermic bladder, that is, a double-walled sac, whose outer wall represents the ectoderm, while the internal gives rise to the epithelium of the mid gut with its glandular appendages. On comparing this with my description of the changes during the corresponding period of development of *L. trapezoides*, considerable differences will be noticed. I do not believe that essential errors can have occurred on either side; there must be a real difference in the facts observed, and this is, in part at least, explained by the peculiarities of the later development of *L. trapezoides* to be now described.

Immediately after its formation the germinative sphere does not show a well-determined arrangement of the cells, though there are differences in size between them. With regard to the quality of the protoplasm it is the same in all the cells. But after some time a grouping of the cells into distinct layers begins, which leads to the formation of the germinal layers. The peripheral cells about one of the poles multiply and become flatter, but it is to be noticed that two of them—those situated at the most prominent point—do not take part in this, but, on the contrary, increase in size, and attain a considerable length; these cells then become covered by the small peripheral cells, and pushed towards the centre (Pl. IX, fig. 3, *cm.*). In the inside, upon these large cells, which I shall call mesoblastic, rests a layer of small and flattened cells (*en*), and at their sides are already distinguishable a small number of very thin flatter-shaped cells (*mes*); these cells are closely united together and arranged in two rows, which are directed from the sides of the cells (*cm*) towards the opposite pole, where they meet the remains of the embryoplastic material, consisting of a layer of large and still undifferentiated cells. Thus, the constitution of the laminæ of the germinal layers is in part marked out; the flat peripheral cells (*ec*) form the external layer (ectoderm), those collected in the interior produce the internal layer (endoderm), and the few cells grouped in two lateral columns (*mes*) are the first rudiment of the middle layer (mesoderm); all the large cells occupying the other hemisphere undergo further changes, tending to produce an arrangement completely corresponding with that just described. But before this occurs a division of the germ into two hemispheres always becomes evident. While the egg is elongating in one diameter a transverse furrow appears half way between the two extremities; it does not,

however, extend round the whole circumference, but is present on one side only. This furrow, deepening itself, either by the elevation of its borders or because the cells lining its floor force themselves into the lateral elevations, divides the germ nearly completely into two halves, which are joined only by a series of enlarged ectoderm cells. The process of the development of the transverse fissure goes on simultaneously with the differentiation of the cells of the hitherto inactive hemisphere.

To explain better the entire process I will describe figures 4, 6, and 7 of Pl. IX. Comparing fig. 4 with fig. 3, which represent two stages very near together, the elongation of the diameter which passes through the poles of the egg will be noticed, transforming it from a sphere to an ovoid; at one extremity the arrangement of the cells remains exactly as it was in fig. 3, but in the middle the mass of cells is divided by a larger fissure, which represents the bottom of the transverse furrow; to the right of this is seen, instead of the simple layer of large cells of fig. 3, two very distinct groups of cells, one peripheral, of nearly cylindrical cells, and a mass of polygonal cells in the interior, which forms part of the wall of the furrow.

In fig. 6, which appears a little less complicated in detail only because the plane of the optical section does not pass through the rudiments of the middle layer, which are, however, easily recognisable in the preparation, the division into two halves of like structure may already be distinctly seen, though that on the right hand is still a little behind the other in development, not having the endoderm well defined. Of the two mesoblast cells on this side one only is represented, because the other is hidden by it. In the middle, between the two hemispheres, are to be noticed two large, transversely elongated cells, distinguished by the clearness of their protoplasm, which form a kind of ligament between the two halves.

Fig. 7 shows the egg distinctly divided into two halves of very similar structure, joined together not very closely by a median cord of large cells containing large nuclei.

While the transverse furrow deepens the entire egg changes its form and becomes kidney- or bean-shaped, and then the free margins of the groove arch inwards and approach one another in such a way as to narrow considerably the entrance. The bottom enlarges in the direction of the extremities and excavates the inside of each of the hemispheres, pushing the cellular layer (*en*) towards the inside. In other words, the endoderm becomes invaginated,

beginning at the lateral margins of the furrow in both the hemispheres, which are thus transformed into sacs with double walls. This form of the embryo is represented in profile in fig. 8, and in front view of fig. 9, where the relations just described can be easily made out. Each of the compartments encloses a cavity (*cd*), which communicates with a common space opening to the exterior by a fissure, already much contracted, in fig. 9. The walls of each compartment consist everywhere of two or more layers of cells, a very distinct ectoderm (*ec*) and an endoderm (*en*); besides this, there are at the opposite extremities of each two mesoblast cells (*em*) and two rows of flattened cells (*mes*). Each of the lateral cavities (*cd*) will form the digestive cavity of an individual, their openings into the common groove will each become a mouth, and the single egg will produce two worms. To come to the end at once I will explain the manner in which the perfect separation into two individuals is accomplished. It is very simple; each embryo rotates about the axis of the uniting cord towards the side opposite the common aperture, and turns at the same time a little on its own long axis, but in the opposite direction to the movement of the other; from the first movement results the enlargement of the aperture and of the common cavity, which leads to their complete separation and the approximation of the sides of the two embryos, united by the median cord in such a way as to leave them nearly parallel with one another.

The second rotation produces a want of symmetry between the planes of the longitudinal sections; that is to say, the corresponding meridians of the two embryos intersect nearly at a right angle. The point where the uniting cord holds together the two embryos corresponds to their necks, since it is between the cord and the oral apertures (which are now much restricted and converted into narrow canals) that the two cephalic lobes take their origin.

In this union the two embryos, forming a rather monstrous twin organism, remain for some time, growing and developing and completing their internal organisation, turning gently in the albumen, without at all impeding one another, by the concordant action of their vibratile cilia, which have been some time developed. But little by little the commissure relaxes to such a degree that the least pull is enough to break it, a circumstance which can hardly fail to occur when the contractions of the bodies of the embryos begin. It thus happens that the Siamese twins dissolve their too close relationship, which had probably become a nuisance to each

of them, and abandoning each other rove at their leisure through the albumen. But affairs do not always go on smoothly. There are cases, not at all rare, in which this strange mode of development leads to true monstrosity; this happens when the uniting cord does not relax in time to be able to be broken, or when it extends to an abnormal amount. In fact, among perfectly developed worms already hatched double monsters are met with in all grades of concrescence (more or less perfect), from those that are so firmly united along the whole extent of the body that it is impossible to separate them without breaking them to pieces, to others which are hatched coupled together, but only by so thin and frail a ligament that they yet succeed in effecting their separation, although it may be at a comparatively late period. All, however, have two heads and two tails, two mouths and two ani, well separated; it appears also that the junction never extends to any internal organ, but always remains confined to the epithelial layer of the body-wall.

The above-described mode of formation of the twin embryos is realised in the great majority of cases, but not seldom embryos are found in other conditions, differing chiefly with regard to the age at which the twins are produced. We have seen above how the differentiation of the layers of the blastoderm begins at one pole while the embryoplastic material of the other hemisphere is still in an undifferentiated state, but yet that this inequality disappears very soon. There are, however, cases in which a single embryo attains a considerable development before the first rudiment of its companion is formed. I have represented one of them in fig. 5; it is to be understood that this is much further developed than fig. 4. The endoderm has already its peculiar appearance and forms a closed sac; the germinal streaks are very distinct, although the example lacked any sign of a second embryo if the large cells, which are obviously identical with those of the uniting ligament, do not indicate that a second individual may yet grow out. In fig. 10 is seen a much more advanced embryo, in which, above the opening of the mouth, a small cellular excrescence (x) of a rather irregular form appears, which passes without interruption into the germinal streaks, and is the rudiment of the second embryo. I have found also much further developed embryos, which produced similar buds on the margins of their mouths. On the other hand, I believe the case to be most rare of an egg giving rise to only one embryo, or rather, I should say, I have never ascertained the existence of such a case. It is quite true that sometimes a single worm escapes from a cap-

sule, but then nearly always the remains of its companion are found.

This mode of reproduction appears to me worthy of some remark, although it is not my intention to enter here into a discussion of the known facts of development of other animals which might be compared with it. Apparently in our case there is not a succession of individuals, in which only the first owes its existence to the co-operation of the sexual elements, while the other takes its origin from it by agamic generation; from the egg of *L. trapezoides* two individuals arise directly and essentially independently of one another. In the cases described last, in which a well-developed embryo produces the rudiment of the other, the second should be considered to be a bud, but such a case is abnormal; regularly, the second embryo, although formed a little later, and in connection with the other, does not develop from the embryoplastic material employed in the formation of the first, but from a portion of the blastomeres derived directly from the segmentation which remains intact until it becomes an independent formative centre.

To interpret the division of the embryoplastic material as the expression of a fission that happened at first in the adult animal and then, in the course of generations, became put back by the help of natural selection to the beginning of development, would be to make a very arbitrary and little satisfactory hypothesis, which also would be in antagonism with the knowledge that we have of the fission and germination of the annelids. As far as we know, this process takes place regularly in the posterior part of the body (not at the head end), and this is not merely an empirical law, but is explained by the fact that in many annelids the posterior extremity retains during life distinctly embryonic characters. Hence there is no more probable explanation of the doubleness of the embryos than what can be found in the original internal arrangement of the fecundated egg, a thing which is not so strange, since the experiments of Haeckel on the Siphonophoræ[1] have shown the possibility of multiplying the number of embryos by artificial division of the first mass of blastomeres. Nevertheless, the case we have before us appears to be without analogy in the development of other animals.

Todaro established, three years ago, that the individuals of the compound stock of Salpa are to be considered, not as children, but as younger brothers of the solitary stock; how

[1] 'Zur Entwickelungsgeschichte der Siphonophoren.' Utrecht, 1869, p. 78.

great soever may be the difference between the mode of production and the anatomical and physiological relations of the two alternate generations of Salpa and the gemelliparous development of *Lumbricus trapezoides*, it is not possible to fail to see the same principle ruling in both these forms of development. Todaro was led to the conclusion that the explanation of the phenomenon is to be sought in the earliest steps of the process of sexual reproduction.[1]

The following considerations may, perhaps, suggest a means, a little difficult, however, in the application, for solving the question definitely. The important labours of Fol[2] and of Hertwig[3] have rendered it very probable that not only is the introduction of a single spermatozoon into the protoplasm sufficient to establish an orderly and efficient generative movement, but that the presence of more spermatozoa, instead of assisting the development, occasions a serious disturbance of the order of the molecular arrangements, producing a number of centres of activity, and thus leading to an irregular segmentation, and at last to the complete destruction of the embryoplastic material. Now, the thought naturally presents itself, that in some case the action of two spermatozoa introduced into an egg of great vitality, regulated by means of special dispositions, might augment instead of turning aside and paralysing the productive force of the egg, inducing in it a transformation not, as is usual, into one, but into two perfect embryos, and this might be the case in *Lumbricus trapezoides*.

The fact that each capsule of *L. trapezoides* produces two worms was known to Dugès,[4] who also observed and figured a double monster; and Ratzel and Warschawsky describe a like abnormality in *L. agricola*. It is a pity that the description which these authors give of the first stages of development is too superficial to allow a precise conception of them to be made.[5]

This double reproduction is exceptional even in the single genus *Lumbricus*. *L. teres* follows the ordinary rule, producing one embryo from an egg and no more; the same holds good, without doubt, for *L. rubellus*.

As the duplicity of the embryos has no influence on the

[1] 'Sopra lo sviluppo e l'anatomia delle Salpe.' Roma, 1875, p. 68, cf. Hatschek "On Pedicellina," 'Zeit. für Wiss. Zool.,' T. xxix, p. 530.

[2] 'Sur le commencement de l'hénogénie.' Genève, 1877, p. 25.

[3] 'Morphologisches Jahrbuch,' T. N., 1878, p. 172.

[4] 'Annales des Sciences Naturelles,' T. xv, 1828, pp. 331—332.

[5] Loc. cit. The processes described in this work as the first phenomena of development belong, as Kowalewsky has justly observed, only to the degeneration of the non-fecundated eggs.

internal development, I shall take no more notice of it and I shall treat of each embryo without heeding its companion. We left the embryo in the form of a depressed globe, now it is lengthened in its antero-posterior diameter, and a little compressed on the dorsal and ventral surfaces, and hence has the shape of an oval lens. The central cavity enlarges because it begins to suck in to itself part of the albumen in which the embryo swims. This nutritive substance does not become employed and transformed immediately into the growing tissues, but, drawing itself together, forms a large and dense mass, which nearly completely fills the space. The mouth, although it serves as a passage for the introduction of the albumen, becomes diminished to a very fine canal, which pierces the body-wall obliquely from below upwards. Sometimes it shuts completely, and then, being without the means of absorbing the albumen, the embryo remains very small and the lumen of the canal disappears, its walls approaching each other till they touch. Notwithstanding this, all the tissues develop regularly and arrive at perfection, if in the subsequent changes the mouth reopens.

The Germinal Layers and the Germinal Streaks.

The way in which the blastomeres of one hemisphere become arranged in distinct layers, while the common rudiment of the two embryos is still a solid sphere, has been described above. The ectoderm (*ec* in all the figures) becomes defined by the separation of a single layer of cells around a solid central mass. Its cells from the first are cylindrical, with rather dense protoplasm, containing a great number of very fine granules. As the embryo increases in size the cells multiply and, losing their cylindrical form, become transformed into very broad and thin plates, which cover, as a single layer, the whole body of the embryo. In the middle line of the ventral surface a double or treble row of these cells, stretching from the aboral pole to the mouth, developes a great number of vibratile cilia, which produce by their movements the continual gentle rotation of the embryo about its transverse axis.

The formation of the endoderm (*en*) is not so simple and easily explained. It appears possible, even probable, that when the germinal bladder (fig. 2) becomes solid some of the lower and smaller cells of one pole enter into the segmentation cavity; but, on the other hand, there is no doubt that other cells, which participate in the formation of the inner layer, separate themselves from the central ends of the long cells surrounding one side of the segmentation

cavity (figs. 3, 4, 6, 7, *en*). It is certain, then, that before the hollowing of the embryo by an invagination, which produces the digestive cavity and the mouth, the layer which is to become the endoderm is already easily recognisable. At that time, however, the aspect of all the cells is still uniform, but when the invagination begins, a peculiar change occurs in the endoderm cells. They increase much in length, and become prismatic; their nuclei approach the extremities and project freely into the digestive cavity; the protoplasm becomes soft and filled with numerous albuminous corpuscles, a sure sign of the active nutritive changes going on in it. In this stage the endoderm cells, which never bear vibratile cillia, do not cover the digestive cavity alone, but also line the buccal canal as far as its external opening (figs. 8 and 10).

Mention has already been made of two cells of the peripheral layer, which become pushed into the interior, and then covered by the flat cells of the ectoderm. This happens near the aboral pole on the side which afterwards becomes dorsal. They are very easily recognised when their external surfaces still project freely on the surface by their size and by their rather more dense protoplasm, and in the figs. 3 and 4 (*cm*) the way in which they become gradually covered with flattened cells, which extend from all sides towards a point of union, is seen. In figs. 6, 7, 8, 9, *cn*, they are completely covered and have moved further inwards. Their longitudinal section is wedge-shaped, with the thin end diverted towards the periphery, and the base bordering upon the layer of endoderm. They each contain a large spherical nucleus.

At the sides of each of these cells, between them and the ectoderm, appear very soon two or three small, very thin, disc-shaped cells placed one upon the other, with their bases firmly adherent (figs. 3, 4, *mes.*) These cells, increasing rapidly in number, group themselves in two rows or cords, which, starting from the mesoblasts, are directed immediately towards the opposite edges of the lentiform body, where they turn up to join the oral extremity (figs. 5, 8, 9, 10, 11*a*, 11*b*, *mes*). They thus together make a nearly complete circle, interupted only behind by the two interpolated mesoblast cells, and in front by the mouth; they do not remain long in this state, but first widen and then become thicker, being now composed of two, three, or more rows of cells, placed side by side, and of as many layers placed one upon the other (figs. 11*a*, 12, 13). These cellular arches are the rudiments of the mesoderm.

Now, what is the origin of the cells of the mesoderm? According to Kowalewsky, the two large cells produce the middle layer in *L. rubellus*, while in *L. agricola*, where such cells do not exist, the well-developed endoderm probably furnishes the material for the formation of the mesoderm. In *Euaxes* the middle layer is derived directly from the division of the four first blastomeres.[1] Hatschek affirms still more decisively that in *L. rubellus* the mesoderm is derived from the two large cells.[2]

There is no doubt that the mesodermic arches begin with the appearance of the few small cells at the sides of the mesoblast cells, and that their development proceeds from here towards the opposite extremity; this is certainly a remarkable fact, but is it enough to enable us to decide the part which the large cells play in the formation of the mesoderm? I have not met with states of incomplete division in the latter, but very little value can be attributed to such a negative result, especially because it is matter of general experience that, in rapidly growing tissues, cells in which the process of division has really begun without being completed are rarely observed. This fact may be explained by the rapidity of the process of fission, after the previous internal changes have been effected. But the observation that the large cells retain their volume apparently unaltered from the beginning to the end of the embryonic life may raise more serious doubts as to their reproductive activity.

At least I have not been able to *make sure* of the existence of oscillations in the size of the large cells which would have justified the supposition that they deprived themselves of a portion of their substance to give rise to the cells of the mesoderm. Kowalewsky represents a stage in which each of the large cells is divided into three smaller ones of nearly equal size.[3] In *L. trapezoides* this never happens; on the contrary, the cells of the mesoderm, which are in contact with the large cells, are always among the smallest and most compressed. Notwithstanding all this I am also of opinion that there must be a production of new cells from the two large ones, solely because they show very often the phenomena which may be considered with great probability as a necessary preparation antecedent to the formation of new cells. In this case the mode of reproduction would be what is ordinary called gemmation; cells greatly inferior in size to the mother-cell would separate themselves from a point of the surface, and the mother-cell

[1] Loc. cit., pp. 16, 23, 29.
[2] 'Zeit. für Wiss. Zool.,' T. xxix, 1877, p. 545.
[3] Loc. cit., pl. vi, fig. 14.

would regain almost immediately its original volume, by the aid of an extraordinarily energetic nutritive change. Now, the cells produced in such a way from the large ones certainly would not be placed elsewhere than in the mesoderm, and would form a part of it. I say, a part, because another, and I believe the larger part, certainly has a different origin. It has been explained above how the ectoderm cells transform themselves into wide and flat plates; this is true for the dorsal and ventral surfaces, but the cells of those tracts of ectoderm which cover the cords of mesoderm either keep their longer or shorter prismatic or cylindrical shape or recover that form after having been depressed before the mesoderm comes to raise them (figs. 11*a*, 11*b*, 12, 13, *ecc*).

Now, while the larger number of the ectoderm cells show little activity, and appear not to divide, except when their is no other way to prevent the interruption of continuity of the external covering of the embryo, those which cover the middle layer are in a state of the most rapid reproduction. The newly made cells do not become employed in the enlargement of the surface, but losing little by little their connection with the layer from whence they took origin, they force themselves inwards, when they unite with the cells of the mesoderm. This relation appears to me to be very easily and clearly recognisable. Sections, especially transverse ones, show how, here and there, the line of demarcation between the ectoderm and mesoderm disappears altogether, while in other parts of the same embryo it is very evident. It is impossible to decide whether certain cells belong to the external or to the middle layer; indeed, it sometimes seems that the covering of the two cords is folded inwards round their proximal margins, cells of the external layer in this manner placing themselves below the already formed elements of the mesoderm. But the direct production of mesoderm cells from the external layer lasts only a short time. With the progress of development a very distinct demarcation becomes established between the two layers, and the very important increase which the mesoderm henceforward undergoes is produced solely by the multiplication of its own proper cells.

On the other hand, with the greatest attention, I have not been able to discover the least sign of the endoderm cells participating in the formation of the middle layer, and as in the stages under consideration their relative positions are very clear and distinct, I do not hesitate to say that the internal layer has no share in the formation of the mesoderm. But how can this be? I have admitted, at least for a part of

the mesoderm, an origin from the two large cells, and these, according to Kowalewsky, were originally elements of the endoderm, from which they separated and approached nearer the surface. In this case the large cells would merely be the part which unites the mesoderm with the endoderm; and the derivation of the first from the second, though not direct, would be none the less a fact. But, as is indicated in what precedes, I am unable to agree with the assertions of the Russian embryologist, because in *L. trapezoides* the mesoblast cells are distinguishable before the arrangement of the embryoplastic material into distinct layers is recognisable; because at first these cells occupy a position on the surface, with a large part projecting freely, and, changing their position, become pushed from without inwards, instead of coming from a deep layer to the surface; and, finally, because in no respect, neither in the quality of their protoplasm, nor of their nucleus, do they show any resemblance to endoderm cells. After this they should certainly be considered ectodermic elements, if the earliness of their appearance, before the definite foundation of the layers, did not render the question almost insoluble. Besides, I am not at all convinced that the affair takes place in *L. rubellus*, as Kowalewsky supposes; the figures which should bear witness to his assertion[1] do not persuade me at all, and unless he is supported by less equivocal observations I think that his opinion rests on a very doubtful foundation.

I shall call the two cords or mesoderm, together with the superposed ectoderm, the "germinal streaks" (Keimstreifen), and shall use this term to make the topographical descriptions simpler. In tracing the true origin of the organs it would not be correct to use it, as each streak is composed of two layers of different value, of which the lower, the mesoderm, has precise limits, while the upper, the portion of ectoderm belonging to the "streak," is continuous with the general covering of the body. In treating of the original derivation of an organ I shall always go back to the primitive layers.

The germinal streaks, when they have reached the head end, must naturally be closely approximated, since they extend over an oval body. But they do not unite at once, but, ceasing to progress, they widen so as to form two projections, like the heads of nails, at the sides of the mouth. (Pl. X, fig. 15 *pp*). A little later, however, the most anterior cells tend from both sides towards the median dorsal line, and when they reach it fuse with those of the

[1] Loc. cit., plate vi, figs. 10 and 12.

opposite side; a semicircular commissure is thus formed, situated on the back between the mouth and the cells, which unite the two embryos. Figs. 16 and 17 represent sections of the head end, in which the formation of the commissure of the streaks is already completed, and its position relatively to the surrounding parts is easily recognisable. Fig. 16 *b* is a tsection immediately behind fig. 16 *a*, and serves to show the continuity of the cephalic arch or commissure with the cords which occupy the lateral parts of the body. But if in the first stages the enlargement of the streaks is owing chiefly to the junction of cells derived from the ectoderm with the mesoderm, this holds good, above all for the formation of the commissure. It is certain that only a very few cells preformed in the mesoderm enter into this; the larger part are derived directly from the ectoderm, which thickens, until three or four layers of superimposed cells appear (fig. 22 *pc*), the deepest of which then separate themselves from the more superficial to become blended with the mesoderm of the lateral germinal streaks.

Rathke speaks of the origin of the cephalic portion of the germinal streaks in *Nephelis* and *Clepsine* in such vague terms that it cannot be clearly understood,[1] and Kowalewsky does not make any explicit statements on this question, but he figures an embryo of *Euaxes*, in which the union of the germinal streaks on the back is perfectly clear. Lastly, C. Semper, after having found a special germinal streak for the formation of the head in the reproduction by fission and gemmation of the Naidæ, describes also in *Clepsine* the origin of the cephalic streak from two lateral thickenings, which are at first independent of each other and of the ventral germinal streaks, and therewith strengthens his theory of the original distinction between head and trunk. In opposition to this I affirm that in *Lumbricus trapezoides* there is never a special rudiment for the preoral ring, but that the cephalic lobe, whose subsequent changes are so important, is formed simply by the union of the germinal streaks on the back.

This dorsal commissure, which I shall henceforward call the cephalic germinal streak, becoming greatly thickened, raises itself above the mouth in the shape of a semilunar fold or incomplete ring. After this the entrance to the digestive cavity, which till now was a small fissure sometimes very difficult to recognise, becomes transformed into a semicircular fossa, deep at the dorsal side, where it is surrounded by the projecting cephalic germinal streak, and

[1] Loc. cit., pp. 29, 95.

becoming shallower as it approaches the ventral surface (Pl. X, fig. 22). At the same time that this fossa is being excavated, the simple layer of ectoderm covering the cephalic germinal streak folds itself round the edge of the projection and is reflected into the buccal fossa, which till now was lined with large endoderm cells (Pl. IX, fig. 10; Pl. X, figs. 22, 23, 24, *e o*). The inbending begins at the dorsal surface, and extending from here embraces little by little the sides, and finally the ventral portion of the fossa. Thus, the ingestive canal, which anteriorly represents the mouth, but posteriorly is converted into the œsophagus, becomes covered by a plaster of ectoderm cells instead of its original endodermic covering, which is thrust towards the bottom of the digestive cavity. The newly formed epithelium of the mouth and of the œsophagus consists of a single layer of slightly granular, cylindrical cells, elongate in the interior, but becoming shorter as they approach the edge of the fold, where they are continuous with the external covering of the body. They soon put out vibratile cilia, very similar in form and movement to those already described on the ventral surface. A similar covering of cilia extends now also over a circle of the external ectoderm surrounding the mouth.

The vibratile cilia in the embryo of *Lumbricus* are thus confined to the tract of ectoderm cells which is situated on the ventral surface between the germinal streaks, and extends from the mesoblast cells at the aboral pole to the cephalic extremity, where it unites with the vibratile ring just described. This mode of distribution of the ciliated cells, which remains unaltered for nearly the whole of embryonic life, calls to mind that, not of the larvæ properly so called, but of the young stages of many, and the adult of not a few, Chætopods.

It is obvious that, as the germinal streaks lengthen, their respective positions, as well as the general shape of the embryo, must alter, and the necessary changes take place, as is always the case in the mechanism of the animal body, according to the principle of least resistance. In fact, instead of producing directly the lengthening of the embryo (to which, perhaps, the endoderm and ectoderm, which at this period only follow passively the movements of the germinal streaks, would offer too much resistance); the streaks seek to meet the increasing need of space by leaving their lateral symmetrical positions and placing themselves on the convexity of the ventral surface, about a radius of curvature which constantly becomes smaller; at the same time their points of origin, that is to say, the two large cells,

become moved more on to the back and towards the oral extremity, in such a way that, in some sections through the posterior portion of the embryo, the transverse sections of the two streaks are found at the lower part and at the upper part the two large cells, together with the last part of the streaks (Pl. IX, fig. 12). Leaving this point, on the dorsal surface, the germinal streaks descend abruptly downwards, embracing a somewhat triangular space at the top of the posterior extremity, and, having reached the ventral surface, approach, with their convexities, both each other and the median line, without, however, adhering or coming into mutual contact. Figs. 11, 12, 13, and 14 of Pl. IX make this process of displacement quite clear. Thus approximated to one another the germinal streaks stretch along the ventral surface, but at the anterior part of the embryo they again separate, and arching over the lateral surfaces, ascend on the back to join in the cephalic commissure.

Besides this displacement, the development of the germinal streaks must cause gradually an alteration in the general form of the embryo, and the more so since the streaks grow, not only in length, but also in width and depth. Hence the transverse section of the body loses its lens shape and becomes circular, then the ventral surface becomes more and more convex, and the anterior and posterior ends, curving towards the dorsal surface, this becomes depressed and concave, so that the embryo assumes a kidney or bean shape.

Turning to the development of the cephalic germinal streak, we find the mesoderm separated completely from the ectoderm, consisting of a mass of small roundish cells, which fills completely the space between the ascending external lamina and the descending inflexion of the fold of ectoderm. Some time later two narrow fissures appear in the lateral region of this mass of mesoderm, then enlarge towards the median dorsal line, where they then unite with one another, thus splitting the mesoderm into two concentric layers, one external and one internal. But as the split begins nearer the external surface than the surface bounding the œsophagus, the layers are, from the beginning, of unequal thickness; the external consists nearly everywhere of a single layer of cells, while the internal has two or three layers. The first adapts itself to the external wall of the cephalic ring, the second joins itself to the oral epithelium.

The splitting of the mesoderm in the cephalic germinal streak is followed by an analogous process in the ventral germinal streaks, beginning from the front and progressing gradually towards the posterior end. About this most

important event, on which is in great part founded the typical structure of the body both of Annelids and Vertebrates, I shall only say a few words, because I do not wish to enter here into the consideration of the particulars of histogenesis; I do not know how to do better than to repeat the beautiful and most exact explanation given by Kowalewsky of the process in *Euaxes* and *Lumbricus rubellus*.

In *L. trapezoides*, as in the above-named Oligochæta, the successive division of the mesodermic cords into segments as primitive zoonites precedes the splitting of the mesoderm. It appears that this division happens in *L. trapezoides* at a little later period than in the other species, because when, the first traces of it can be discerned, when, that is to say, the finest transverse lines of demarcation appear between successive portions of the mesodermic cords, these are already very thick and contain two, three, and more layers of cells; the space which divides the streaks in the median ventral line is, on the contrary, still very wide. Hence are formed two parallel rows of transversely elongated, rectangular plates. Afterwards each plate becomes split by a horizontal fissure, so that the mesoderm is divided into two unequal lamina, of which, unlike what we have noticed in the splitting of the cephalic germinal streak, the external is much thicker than the internal, which only consists of a single layer of cells (Pl. IX, fig. 13). And as the splitting does not pass beyond the limits of the primitive zoonite, nor reach to its boundary line, the cavity remains surrounded on all sides by mesoderm cells; each primitive zoonite is transformed into a compartment, or rather, into a four-sided prismatic case, with a central cavity whose external wall is thickened, while the internal consists of a single layer of cells. The anterior vertical wall of each compartment adheres firmly to the posterior wall of the segment in front of it, and thus are formed the septa, stretched between the body-wall and the intestine. They are thus at first each composed of two layers belonging to two adjoining zoonites; then, in consequence of the strong tension which they have to sustain, the cells group themselves into a simple, very thin membrane, which is not placed vertically to the long axis of the embryo, but goes obliquely from behind forwards. Hence, in almost all perfectly vertical transverse sections, are seen on each side two separate cavities; the ventral is the posterior part of a segment and the dorsal the anterior part of the following segment; the row of cells which divides them is the oblique section of the septum. Not rarely two cavities are formed in the same primitive compartment, but they soon unite. Later,

the septa become perforated in many points, the cavities of the primitive somites communicate freely and form together the general "somatic" or "body" cavity.

Of the horizontal walls of each zoonite the external is placed beneath the ectoderm, the internal encircles the epithelium of the digestive cavity. The external layer resulting from the splitting of the mesoderm is called the somatic lamina, the inner the splanchnic lamina; their origin and the part they play in the formation of the body leave no doubt of their homology with the layers of vertebrates, distinguished by the old and somewhat inappropriate terms fibro-cutaneous (Haut-faser-blatt) and fibro-intestinal (Darm-faser-blatt). This is an agreement of the highest theoretical importance, because the analogy in the development of the primitive zoonites, of the somatic cavity, and of the somatic and splanchnic laminæ, shows with surprising clearness the close relation between the vertebrates and annelids.

Now, it is clear that the differentiation of the cephalic germinal streak is essentially the same as that of the ventral germinal streaks, and differs only in points of secondary significance. The head cavity is formed by the fusion of two lateral fissures, which divide the mesoderm into a somatic and splanchnic lamina. But while the zoonites of the trunk generally embrace the whole circumference of the trunk and close in the dorsal median line to form perfect rings, the cephalic zoonite, which from the first is placed above the oral fossa, is unable to complete itself in the same way, because, when its lateral branches direct themselves downwards and backwards towards the ventral surface they meet the first zoonite of the trunk, and hence the cavities of this zoonite and of the head unite. The anterior end of the head segment becomes more and more prominent, and is transformed into a cylindrical process, the upper lip—a kind of proboscis.

It is evident at the first view, from the chronological order in which the formation of the primitive segments and the splitting of the mesoblast takes place, that the segmentation begins in front and gradually proceeds backwards. But it is still necessary to know whether the first zoonite of the trunk or the cephalic zoonite is the first formed, because Semper has attributed great importance and a fundamental significance in the morphology of all articulated animals to the fact that, in the development of vertebrates and in the organic multiplication of the Naidæ, certain segments of the head appear later than those of the body.[1] The investigation of this point is not easy in the embryos

[1] Loc. cit.

of *L. trapezoides*, because the great curvature of the anterior end of the body, would easily conceal the existence of a very narrow fissure. Notwithstanding this, I am convinced that the splitting of the mesoderm appears first in the cephalic germinal streak; that, namely, the cephalic segment is the first formed, although the first segment of the trunk is formed nearly at the same time.

The splanchnic layer of the cephalic ring, which at first covers only the upper side of the buccal fossa and œsophagus with a thick layer of mesoderm, extends gradually its lateral parts towards the central surface, and embraces the ingestive aperture completely. Then certain cells of its deeper layer begin to migrate into the inflected ectoderm which clothes the cavity of the head intestine, making their way between the bases of the epithelial cells and slightly raising them (Pl. II, figs. 19 *b*, *c*, *d*, 23, 24). This process begins also from the dorsal side, and ends in the formation of strong and thick walls for the head intestine, which by their origin belong to the splanchnic layer of the mesoderm, from which they become distinctly divided. The epithelium becomes reduced to a thin almost cuticular membrane, which in the adult state lines the mouth and œsophagus.

Thus, the walls of the ingestive end of the alimentary canal, at three successive periods of embryonic life, have a structure different both in form and in the origin of the material; at first they are formed of endoderm, this then becomes pushed away and replaced by an inflection of the external covering of the body, and, lastly, they consist nearly entirely of mesodermic tissues, the ectodermic epithelium being reduced to a thin layer of cells fused with them.

It is probable that the transformations of the splanchnic laminæ in the œsophageal tube may correspond in some way with what Semper interprets in the development of the head intestine in *Nais* and *Chætogaster* as the formation of true branchial slits, homologous with those of Vertebrates, which then become converted into part of the œsophageal walls.[1]

Of canals and external orifices I have found no sign in *Lumbricus*, and I have found nothing resembling the branchial apparatus of Semper, unless it is the above-mentioned passage of a part of the splanchnic lamina of the cephalic germinal streak into the walls of the head intestine.

During the time of greatest activity of the mesoderm, until a considerable number of segments are formed, the other two

[1] Loc. cit.

layers keep their primitive state nearly unaltered. The endoderm shows no other change than the enlargement of its cells filled with numerous granules of dense albumen, and the displacement of their small oval nuclei towards the free surface. The reproductive activity of the ectoderm appears to be confined to the production of the secondary epithelium of the head intestine; in its other parts the cells become very much more stretched out into thin plates by the increasing internal pressure, which is greatest on the dorsal surface, where they become so thin that it is sometimes difficult to recognise them. They retain, however, their nuclei, placed in small thickenings, which project inwards, taking advantage of the less resistance at the lines of separation of the endoderm cells.

But when the anterior zoonites are marked out, the ectoderm resumes its reproductive activity, the first and most important result being the formation of the central nervous apparatus.

Development of the Cephalic Ganglion.

The investigation of the first stages of the development of the supra-œsophageal or cephalic ganglion is rendered specially difficult by the rudiment being situated on a strongly curved projection. In investigating the differentations in a very small space, and of a tissue composed of very small cells, only the very thinnest possible sections are of use, which, to render the relations of the surrounding parts intelligible, must pass exactly at a right angle through one of the principal axes of the rudiment, a condition which can only be obtained by chance in transverse sections; in *longitudinal* sections the median one is vertical, but all the others are necessarily oblique; this is even more the case with *horizontal* sections. But since there is no other method of research, I have made sections in all directions; by combining the sections of a series with one another, and with those of other series made in different directions, I think I have formed a fairly precise conception of the way in which the cephalic ganglion is formed.

Fig. 23, Pl. X, represents the anterior part of the exactly median section of a longitudinal series, made from an embryo of about 0·4 mm. in length. The structure of the cephalic ring, already described, is easily recognised; the head cavity, lined by the large splanchnic lamina (*lsp*) and by the somatic lamina (*lso*), here reduced to a very thin layer of fusiform cells. The ciliated epithelium of the mouth (*eo*) is folded towards the external dorsal surface, where it becomes

continuous with the ectoderm, the cells of which are cylindrical on the edge of the projection, but on the dorsal surface from their plates, which appear fusiform in section. But what has lately happened is that for a small space the ectoderm has become thickened; it consists here of two sets of cells, while a short time before it was everywhere composed of a single layer. The cells of this thickening (*gc*) are not, however, arranged in distinct layers, but are closely united into a single mass; it is exactly and clearly limited by the somatic lamina. The unfigured sections of the same series, which are immediately to the right and left of the one described, show the same characters, with the difference only that the number of cells composing the thickening is smaller; the same is observed also in the following sections on each side, although these are very oblique. In the sections still more to the sides the thickening disappears altogether, and the ectoderm becomes again unicellular.

Examining now the head end of a slightly more developed embryo by means of transverse sections, we see in the first (Pl. X, fig. 20 *a*), which passes only through the semilunar projection of the cephalic zoonite, a group of small cells (*gc*), rather thinned in the middle, completely separated from the mesoderm, which is here in an abnormally retarded state of development, not being yet split in the median line, and beginning to separate itself from the superficial layer of ectoderm. The section immediately following this (fig. 20 *b*) shows how these cells pass directly into a very conspicuou enlargement of the ectoderm in the median dorsal line, which here is composed of as many as four layers of cells. In the third (fig. 20 *c*) the thickening of the ectoderm, although diminished in the median line, is increased at the sides, where it descends for a good distance towards the ventral surface, becoming gradually thinner, and at last unicellular. This is shown best in the left side of the figure, the section being a little oblique. In the fourth section the ectodermic thickening may be still seen, though it is much diminished. In the following sections it exists no longer.

The series shown in figs. 19 *a*, *b*, *c*, *d*, is taken from a still more developed embryo. In the first section (fig. 19 *a*) the thickening of the ectoderm embraces, in the form of a half circle, the superior convex part of the cavity of the head (*cc*), from which, however, it is separated by the thin membranous somatic lamina (*lso*). On the external surface of the thickening a single layer of flat pavement-cells (*ec*) is separated from the internal mass, composed of roundish cells with relatively very large nuclei; in other words, the rudiment of

a new organ, the "cephalic medullary plate," has become separated from the peripheral ectoderm, which once more forms a unicellular covering. Fig. 20 *b* shows the same arrangement nearly unaltered; but in the third section (fig. 20 *c*), instead of a continuous semicircular thickening, there are two large projections of ectoderm (*gc*), which thrust themselves into the cephalic cavity, separated from each other by a largish tract of simple ectoderm.

These projections are still more conspicious in fig. 20 *d*. At the ventral side are seen in the last section two elevations, formed of small cells very like those of the rudiment of the cephalic ganglion, and separated from each other by a furrow, whose floor is formed of ciliated cells (*m*). This is the section of the rudiment of the first ganglion of the ventral chain. It is important to notice that there is no connection between this and the dorsal thickening (*gc*). In the three following sections the last are still recognisable although much reduced; further back they are altogether absent. Fig. 21 *a*, *b*, *c*, *d*, are longitudinal horizontal sections of an embryo 0·6 mm. in length; 21 *a* is the fifth of the series, going from the ventral to the dorsal surfaces. It is to be understood that when the embyro is placed horizontally the first sections pass through the very prominent belly without touching the mouth or head end. The section is not perfectly at right angles to the vertical axis, but has fallen with its left side nearer the ventral surface than the right, hence the difference. On the left side the ectoderm appears thickened, and this is the section of the longitudinal ventral chain of ganglia (*n*); on the right side and in front the ectoderm consists of a single layer of pavement-cells (*ec*). In the segment which comes next (21 *b*) the ectoderm cells on the apex of the head have become long and cylindrical, but are still placed in a single layer. A little further back the ectoderm shows on each side a spindle-shaped swelling (*gc*), which loses itself again in the unicellular layer covering the body. The same conditions of the ectoderm are seen likewise in the seventh and eighth sections, in which the lateral thickenings are still larger. But in the ninth (fig. 21 *d*) the cylindrical epithelium which separated the swellings in front has disappeared, and these are united by a largish commissure; they form together an arch embracing the cephalic extremity. Finally, in the tenth section (fig. 21) no further trace of the lateral thickenings is found; the ectoderm is, on the contrary, much thickened in the middle line.

Now, the comparative combination of these sections will be

enough to give a clear idea of the way in which the rudiment of the cephalic ganglion is developed. In the first place, it is clear that it originates in the ectoderm, and in the ectoderm alone. In a narrow transverse tract, close to the apex of the head, the cells of the simple layer of ectoderm divide, and group themselves into the form of a short and slightly curved arch. This, increasing in thickness and becoming distinctly separated from the peripheral layer of the ectoderm, extends along the lateral walls of the cephalic zoonite, but still more behind, where it ends on each side in a conspicuous club-shaped enlargement; it thus assumes a shape which may be compared to a herniatruss with a cushion on each side, which embraces the upper half of the cephalic cavity and of the œsophagus, being directed obliquely from above downwards and from behind forwards. From the beginning till it has reached a considerable development the rudiment of the cephalic ganglion is without any connection with the ganglia of the ventral chain.

I confess that I expected something different. The nature of the adult organ, the mode of formation of the ventral ganglia ted cord, and more general considerations, led to the anticipation of a double rudiment as the first sign of the central nervous apparatus of the head. But, on the other hand, my observations agree with what was before known of the development of the cerebral ganglion of the *Hirudinea*. This only consists, it is true, of a short notice by Rathke for *Nephelis*, and of a still shorter one by Leuckart for *Hirudo medicinalis*. Rathke affirms that the rudiment of the cerebral ganglion is an arch placed on the upper side of the œsophagus, without connection with the ventral germinal streak.[1] Leuckart also says that the formation of this organ occurs, independently of the germinal streak, by the appearance of a cellular cord, which embraces the buccal aperture and adapts itself to the anterior ends of the streak, without at first uniting with it. He further adds that, in a subsequent stage, two lateral swellings are found united by means of a pretty large commissure, both to each other and to the anterior processes of the first ventral ganglion.[2] These short notices, which do not take account of the embryonic layers, are not founded on investigations carried out by means of sections, and are not illustrated by any figures, certainly

[1] Loc. cit., pp. 48, 51. Recently Reinhardt has upheld the truth of Rathke's observations. 'Zeitschr. für Wiss. Zool.' T. xxix. 1877, p. 248.

[2] 'Die menschlichen Parasiten.' T. i. Leipzig und Heidelberg, 1863, p. 709.

cannot have much authority. They are open to the greatest variety of interpretations and objections, but it is a little too much when Semper, taking advantage of an easily explicable inexactness of expression in Leuckart's notice, twists it in an extravagant manner to make it fit his own observations and speculations. In fact, the mode of formation of the œsophageal collar, which Semper thinks typical for all the Annulata, is not consistent either with the observations of Rathke and Leuckart on the Hirudinea, nor with my own on Lumbricus.

During the gemmation of the Naidæ, according to the above-quoted observer, the ventral germinal streak in the cephalic zone splits into two parts, which grow up on the lateral walls of the œsophagus, arching over towards one another on the dorsal surface. As soon as they have embraced the intestine a portion of them separates itself to form the commissure and the ganglionic substance of the brain; the two halves of the supra-œsophageal ganglion thus formed then fuse to one another in the median dorsal line. This portion of the œsophageal collar is derived from the mesoderm. But then the ectoderm developes to the right and left a kind of bud, which Semper calls "Sinnesplatte," because in it is formed the eye of the Naidæ, which is directed towards the dorsal surface, where it enters into the composition of the supra-œsophageal ganglion. Hence the entire œsophageal collar would be a product of the ventral germinal streak, together with two lateral buds of the ectoderm, without the intervention of a dorsal medullary plate, and thus would be an organ heterogeneous, even in its essential parts, being derived as much from the mesoderm as from the ectoderm.[1] I have no observations of my own on the development of this organ in the agamic generation of the Naidæ, but I know that in a group of animals, closely related to these, the embryonic development proceeds in quite a different manner. In *Lumbricus* the first rudiment of the œsophageal collar is a dorsal medullary plate, which arises independently of the ventral chain and exclusively from the octoderm. I do not know what forms the sensitive plates of Semper, since it does not appear justifiable to identify them with the terminal enlargements of the medullary plate.

Lastly, Hatschek, in opposition to Semper, describes the affair very differently. He says: "The first rudiment of the nervous system is found in *Lumbricus* in those embryos in which the foremost segments are developing the segmental organs. It appears as a thickening of the ectoderm

[1] Loc. cit., pp. 206, 210, and elsewhere.

in front of the oral margin (Scheitelplatte). Soon two filamentous thickenings of the ectoderm begin to extend themselves from the lateral regions of the Scheitelplatte backwards along the sides of the mouth into the neighbouring segments, where they lie on either side of the middle line."[1]

I should agree with this as regards the fact that a dorsal plate arises before any other part of the central apparatus if I were capable of forming a clear idea of what the author intends to express by these words, and if I were convinced that he really has observed the first stages. But the assertion that the ventral medulla is produced from two prolongations of the cephalic ganglion I believe to be entirely erroneous if the probability be admitted that, in two species of the same genus, the principal organs would be formed in the same way.

A few words on the further transformations of the dorsal medullary plate. The whole rudiment separates at once from the ectoderm, and becomes enveloped in a sheath of the somatic lamina. From the anterior median part of the arch start two prolongations, which enter the upper lip, where they appear to become confounded again with the ectoderm, which here is transformed into sensitive epithelium. In like manner, the opposite side of the rudiment sends out processes directed backward, which are broader and longer than the anterior. Thus, the cephalic ganglion seen from above appears to consist of two pear-shaped halves broadly joined in the middle. The two lateral projections which form the dilated extremities of the arch, also separated from the ectoderm, extend gradually as much upwards as downwards, and unite principally with the median arch of the medullary plate. In transverse sections this is seen to embrace already more than half the œsophagus. In the median dorsal line is seen a deep impression where the dorsal blood-vessel is placed; the margins of this groove rise a little, and these bendings descend nearly vertically towards the ventral surface, where they end in very fine extremities without joining the ventral chain. I do not wish here to enter into the description of histological differentiations; I will only say that the transverse commissure which connects the two halves of the arch appears in this stage, and is the first to arise. All the cells on the ventral face become transformed into a finely granular substance, while at the sides

[1] "Beiträge zur Entwicklungsgeschichte und Morphologie der Anneliden," 'Sitzungsberichte der Akademie der Wissenschaften in Wien,' T. lxxiv, 1876, p. 1.

and above a thick layer of ganglionic cells remains. As the extremities of the arch descend, these commissural cords lengthen proportionately, and the ganglionic cells on their external sides become scarcer, so that it may be said that the œsophagus is not embraced by the entire ganglion, but rather by the elongated branches of the commissure. These branches must themselves descend to the ventral wall to meet the first ganglion of the ventral chain, for I have never seen prolongations directed upwards from the latter. But the investigation of this point is extremely difficult, since the lateral parts of the collar are very closely enveloped by the mesoderm, whose cells resemble so closely those of the nervous ring that it is not easy to distinguish them with exactness. Hence I cannot say definitely that mesoderm cells do not at this time enter the lower extremities of the collar (this applies only to the lower extremities, since all the remainder is clearly separated from the middle layer) to take part in the formation of the commissure, but it would be still less possible to prove that they do so, and I think it is most improbable. When, at a relatively very late period, the definite union of the cerebral ganglion with the first ganglion of the ventral chain takes place, this first ganglion, as well as those following, possesses a well-developed commissural trunk with which the cord from the cephalic ganglion appears to be directly united.

The Development of the Ventral Chain of Ganglia.

I began the account of the development of the central nervous apparatus with the cephalic ganglion, because, even if it is not, as I believe, the first part formed, it certainly appears at least contemporaneously with the earliest traces of the ventral chain. It is known that the development of the latter progresses from before backwards, but its first rudiment extends rapidly along the whole length of the embryo, as far as the caudal extremity. On the other hand, the separation of the individual ganglia and their histological development takes place gradually, and much later in the posterior than in the anterior part; while the first ganglia have already attained a state of great perfection, those further back exhibit all imaginable gradations, till we reach the condition of the undifferentiated rudiment. Hence, for the investigation of the first changes, it is best to take early embryos; for that of the following stages much older embryos answer very well, because the most different stages of development, united by the minutest gradations, are found in a single individual.

When the mesoderm of the germinal streak has fused in the median line, the ectoderm is still divided into two lateral sheets by the narrow band of ciliated cells, which runs along the whole ventral surface. The cells of this band, besides being covered with vibratile cilia, are clearly distinguished from the rest of the ectoderm by their transparent appearance, their granular protoplasm being replaced to a great extent by a very transparent substance, and reduced to a fine network radiating from the large nucleus, and a condensed layer on the side which bears the cilia. These cells at first project and form a low crest, but afterwards become raised at the sides, so that a longitudinal furrow appears between them, which I shall call the ventral furrow.

At this time the first trace of the developing nervous cord appears as two thickenings of the ectoderm, immediately on each side of the ventral furrow. These are still so little raised that it is impossible to detect them by looking at the embryo from the front; but transverse sections show that one, two, or three cells have been newly formed in the ectoderm, and are placed partly among and partly beneath the pre-existing cells. There can be no doubt as to their origin, for they are perfectly separated from the mesoderm, while they are united into a single mass with the ectoderm, from which many cells show the most evident signs of being in a state of division. Then, at each side of the groove, one of the deep cells of the ectoderm assumes an appearance rather different from the rest, becoming darker, in consequence of the condensation of its protoplasm; it is still further marked by its broader and more distinct outline, an outline which the other ectodermic cells do not possess. The two cells thus distinguished, separated from one another by the epithelium of the furrow, are the first stage of the ventral cord. Sometimes it appears that two or three ectoderm cells become changed at the same time, but in general the process begins in a single cell. This, however, divides without delay, and then two well-defined groups of two or three cells each are seen in the transverse section, on either side of the ciliated cells (Pl. IX, fig, 14 *n*). In this way are developed along the ventral furrow two cords, broad and clearly defined in front, becoming thinned away behind, where they finally blend with the primitive ectoderm. Here the process of division in the ectoderm cells continues, and hence the prolongation of the cords is principally effected by the addition of freshly separated cells, while the increase of their thickness is produced by means of the cells already transformed; it is not, however, impossible that, in

the region where the cords are already distinctly separated, some adjacent ectoderm cells may assume their specific characters and join them.

From this time the cells of the neighbouring borders of the cords force themselves under the furrow, slightly raising the ciliated cells. They approach the median line, and there those of the two sides unite; thus, the two primitive lateral cords join to form a single lamina, which I shall call the ventral medullary plate, and soon afterwards its cells begin to accumulate at certain points, producing a successive series of zones, alternately alike and unlike. This, as well as what follows, will be best explained by reference to successive transverse sections. Only perfectly vertical sections are of use; in these the sections of the longitudinal muscular fibres appear as circular points

In the section fig. 25 *a*, which, together with 25 *b* and 25 *c*, is taken from the tail end of an embryo 3·0 mm. in length, the junction of the cords has taken place. Beneath the bottom of the furrow *sn* the medullary plate (*n*) consists of a single layer of cells, but is raised immediately to the right and left into two parallel crests, which, becoming gradually lower towards the sides, terminate in a thin lamina. The dorsal surface of the plate is nearly flat, and is covered by a thin layer derived from the somatic lamina (*lso*). Thickenings of the somatic lamina are seen on each side of the plate, and between them and the ectoderm the rudiments of the muscular plates (*m*); above the medullary plate, projecting into the body cavity, is the ventral blood-vessel (*v*), attached to the splanchnic lamina (from which it takes its origin), that envelopes the mid gut (*en*). The section 25 *b*, which immediately follows the last, shows a different arrangement; here the conspicuous elevations at the sides of the furrow are wanting, and the medullary plate is reduced nearly everywhere to two layers of cells; but in the third section (fig. 25 *c*) it has again the form and extension which it had in 25 *a*. Such a succession of thick and thin zones is repeated many times, with the difference, however, that further forward the size of the thick zones is greater, so that they occupy two or three sections instead of a single one, and the differences between the zones become less marked.

On examining a series of sections taken from the middle of the body of the same embryo, the first thing which strikes one is the great enlargement of the medullary plate, which in this stage has, in fact, attained its largest relative dimensions. The ventral furrow has disappeared, and its cells, although still recognisable, have greatly changed their

appearance, in the first place having lost their vibratile cilia. This alteration in the cells of the furrow takes place bit by bit; in the same embryo, both behind and in front, the cells are found in their characteristic form, and show a lively vibratile movement. I thought that the cells might perhaps transform themselves at a certain time to take part in the production of new ones, and then return to their preceding state, but I have not been able to obtain proofs of this. It is certain that they have no relation with the mesoderm cells, which are found here for the first time interposed between the ectoderm and the medullary plate (fig. 26 *a*, *mes*), because these are derived from the somatic lamina, which, beginning in front, forces itself from the two sides towards the median line, and then backwards, separating the rudiment of the ventral medulla from contact with the ectoderm.

The groove in the medullary plate, sometimes very deep, which divided the two elevations has now disappeared, or become reduced to a very small impression. The edges of the furrow do not become united, but, on the contrary, the fossa becomes wider and shallower before vanishing, in conquence of the increase of the medullary cells placed above its floor. The cells which occupy the middle portion of the plate are larger, consist of clearer protoplasm, and have more precise limits than those placed in the lateral portions, from which, however, they are not in any way separated. In the following section (26, *b*), the nervous plate has changed its form a little, its sides are thickened and form two elevations on the dorsal surface, between which is found a wide and pretty deep furrow. The internal structure also shews some alterations, the greater part of the large median cells being changed and aggregated with the small ones. The protoplasm of these is dense, and the nuclei fill nearly the entire body of the cell; they are placed so close together that a high power and great attention are necessary to make out their boundaries; signs of division are frequent. A mesodermic sheath everywhere surrounds the medullary plate.

Further in front (fig. 26 *c*) the rudiment of the nervous chain presents a new form. Till now its lateral wings were elongated, and ended in very sharp points; now they are rounded in such a way that their section is kidney shaped. The histological changes met with here are more important. In the dorsal side appear two small, clear-looking, finely granular spots, which stain feebly with hæmatoxylin. They have not distinct limits, but lose themselves n the surrounding cells, whose outlines become little by

little less distinct; no other fibres are seen, unless faint traces of prolongations of the adjacent cells, visible with a higher power, are regarded as such. These are the rudiments of the fibrous commissures. Fig. 26 *d* shows the plate again in the form which it had further back, but the granular substance of the commissure, which encloses some nuclei, is still more conspicuous than in the preceding section, and the two lateral rudiments are fused in the median line and form the bottom of the dorsal furrow. The sides and the ventral portion consist of a continuous pretty thick layer of cells.

The same succession of such alternate zones repeats itself again several times in the backward direction, then every trace of the commissure is lost, and the medullary plate passes by every gradation to the state of fig. 25. In front similar conditions are observed; here, however, every section shows the presence of a commissure in a stage of very much more perfect development.

To illustrate the subsequent changes I select a group of sections of an embryo of 4·5 mm. in length (Pl. XI, fig. 27 *a*, *b*, *c*, *d*, *e*). In the first preparation (27 *a*) the medullary plate has a shallow impression both on the ventral and dorsal surface. The cells occupy the surface, leaving the median part of the upper side free, and are especially accumulated in the lateral processes; from here they are continued round to the inferior surface, where they unite and penetrate deeply into the interior of the plate, so that this again appears to be divided into two lateral cords, whose centres are composed of the granular substance. Immediately in front (fig. 27 *b*) the plate becomes kidney-shaped. The septum, which projects from the cortical layer of cells into the interior, is much more developed, and divides the commissure nearly completely into two trunks. But in the same section the firm union of the cells is relaxed and they separate a little to the right and left, occasioning the appearance of a kind of vertical fissure, which is more distinct in the centre than at the periphery. This is clearer still in fig. 27*c*. The cellular process penetrates a little less deeply into the substance of the commissure, but the fissure which divides it into two parts is more evident, especially at the centre, where it ends in an enlargement. Further, the whole cellular covering is thickened considerably, diminishing the size of the commissure. But in the following section (fig. 27 *d*) that constriction has entirely disappeared; the commissure which forms a large mass containing some scattered nuclei, is surrounded by a uniform layer of cells. The median thickening of the cellular covering reappears once more in the section (fig. 27 *e*),

end thus begins the repetition of the successive variations just described.

According to these observations the mode of development of the ganglionic chain would be the following:—Some of the ectoderm cells, situated on the two sides of the ciliated furrow, divide and form two parallel thickenings. One, or sometimes two or three, cells, of the newly formed deep layer acquire special characters, and separate themselves distinctly from the superficial layer and from the lateral parts of the ectoderm from which they originated. In this way are developed two cords, completely separated from each other by the cells of the ventral furrow. This is the original double rudiment of the subintestinal central nervous apparatus. Then the neighbouring margins of the cords raise themselves, and approach each other, forming between them a groove, sometimes very deep, but having only a temporary existence. The upper cells of the neighbouring sides force themselves above the groove towards the median line, where they meet and unite with each other; their number increasing the groove becomes little by little flattened out and finally disappears. The primitive cords are thus united into a median plate. As soon as the union has taken place, the cells group themselves into a series of swellings and constrictions. The first represent the ganglia, the second the connecting trunks. Now, certain cells placed beneath the dorsal surface on each side are transformed into an ill-defined granular substance, which gradually extends to the median line and forms the fibrous commissural cord. This developes separately for each segment of the chain, before the single segments become united among themselves by a special conducting tissue. The connecting trunks, which run through the whole length of the ganglionic chain, are formed later, simply by the fusion of the commissural trunks of the successive segments; hence the first rudiments play the part of a common foundation for the transverse and longitudinal commissures, in which afterwards by the development of nerve fibres, a regular apparatus of conducting threads is established. In consequence of the formation of the fibrillar substance, the parts of the nervous plate, which are destined to become changed into ganglion cells, extend on the sides and ventral surface in a more or less thickened, but everywhere continuous, layer.

At intervals, thickenings of this cellular covering penetrate deeply into the interior of the plate. They are formed in part by the central cells, which are not transformed into the substance of the commissure, in part by cells, which

migrate from the ventral surface. Then a fissure appears between the cells of the median septum; at first it is confined to each segment, but later extends the whole length of the nervous chain; this is the ventral fissure of the subintestinal nerve cord of the adult.

My researches have fully confirmed Kowalewsky's important discovery that the subintestinal nervous chain of the annelids arises solely from the ectoderm. Semper's statement that it is made up of an unpaired median thickening of the ectoderm, comparable to the medullary groove of vertebrates, and of two cords of mesoderm, corresponding to the spinal ganglia, is definitely contradicted by the development of that apparatus in the *Lumbricini*. And further, this dogma, which had for its object the reconciliation of the differences in the structure and development of the nervous system, observed in annelids on the one hand, and vertebrates on the other, has missed the mark, since we have learned from the excellent researches of Balfour that the spinal ganglia of vertebrates are not derived from the mesoderm.

Semper has already found an opponent in Hatschek, who upholds for *Lumbricus* the origin of the entire ganglionic chain from ectoderm. But, beyond this, his own not very clear descriptions appear to me to be erroneous. We have already noticed that, according to this author, the ganglionic chain is formed from two prolongations of the cephalic medullary plate; that is to say, only the lateral parts of it, parts, which he calls lateral cords, since a medullary groove, very similar to that of the vertebrates, is then formed between them. It is true that in the development of the medullary plate a fissure, sometimes a very deep one, is seen (or), rather there are two, differing in time of appearance and in mode of formation. To my view Hatschek's figs. 2, 3 and 4[1] would represent the first. But here certainly is not a case of invagination; the groove besides is only the space which from the beginning separated the primitive cords, deepened in consequence of the great thickening of their neighbouring sides. With the development of the medullary plate this groove disappears. On the other hand, the fissure in fig. 6 cannot but be the second, whose formation we have described above, and which accordingly has nothing to do with the first. But what I do not know how to explain is the fact that Hatschek represents the walls of the fissure as being very obviously separated from the lateral cells of the plate; in *Lumbricus trapezoides* there is not the least trace

[1] Loc. cit.

of this. The secondary groove may, perhaps, be compared to the posterior fissure of the spinal cord of vertebrates, but certainly not to the primitive medullary groove.

Here I will end, merely adding further, that at the time of the differentation of the first cells of the medullary cords the muscular fibres appear at their sides. The rudiments of the segmental organs resemble those of *Euaxes*, represented by Kowalewsky, and do not develop from the septa, as the same author states that they do in *Lumbricus rubellus*. I confess also that I should not have hesitated to describe them as invaginations of the ectoderm, if the very clear figures in the above-quoted work had not obliged me to investigate the the subject from this point of view. Of the formation of the colossal fibres, which Kowalewsky believes to be homologous with the notochord of Vertebrates, I know nothing, but what Semper describes as the notochord of the Naidini is certainly nothing but the cells of the mesodermic sheath, surrounding the nervous chain.

It is not possible to overlook the great similarity between the development of Annelids and Vertebrates, especially in the formation and transformation of the germinal streak. There would be no great inaccuracy in saying that the belly of Annelids is homologous with the back of Vertebrates, were there not serious divergences shown in the development of the neuro-muscular apparatus, which certainly are not diminished by the discovery of the independent origin of the cephalic ganglion. I, however, believe that every well-recognised fact, although it may be such as to appear to open an abyss between two so-called types, is in reality a step in advance towards the establishment of the unity of the organisation of the animal kingdom. I must defer general considerations to a second part of this work, in which I shall treat of the further development of the Earth-worm, and more especially of the formation of the tissues.

The NEMATOID HÆMATOZOA *of* MAN.[1]

By TIMOTHY RICHARDS LEWIS, M.B., Surgeon, Army Medical Department; Fellow of the Calcutta University. With Plate XII.

THE literature of this subject dates from the period of the publication in 1872 of a paper submitted by myself to the Government, entitled 'On a Hæmatozoon in Human Blood.'[2] Towards the beginning of July of that year, I found nine minute nematoid worms in a state of great activity on a slide containing a drop of blood from the finger of a Hindoo. They were about $\frac{1}{75}$" in length, and $\frac{1}{3500}$" in width, or slightly less than the average diameter of a human red blood-corpuscle (·3 mm. × ·007 mm.).

Unfortunately, after the observation had been made the man could not be found so as to be questioned as to his past history, so that the pathological conditions which might have been associated with this, the first recorded instance of the existence of nematoid hæmatozoa in man, must continue in obscurity.

This observation was, however, followed by several others which have gone to show that the presence of this particular helminth in the blood is very generally associated with Chyluria and with an allied affection known as Lymph-scrotum or nævoid elephantiasis. The extent of this connection may, in some degree, be inferred from the circumstance that whereas filariæ may occasionally be observed in the blood of persons apparently free from disease of any kind, they are, so far as my personal experience goes, invariably present when either of these diseases exist. It must be recollected, however, that the search for them sometimes involves very considerable labour.

These parasites, or parasites very closely allied, have now been found in human blood in many parts of the world. Dr. Prospero Sonsino,[3] in January, 1874 (having no knowledge of previous observations of a like character), found them in the person of a Jew lad at Cairo. They have been found in China by Dr. Patrick

[1] This article forms a portion of a paper entitled "The Microscopic Organisms found in the Blood of Man and Animals," which is shortly to appear as an Appendix to 'The Fourteenth Annual Report of the Sanitary Commissioner with the Government of India.'—ED.

[2] 'Eighth Annual Report of the Sanitary Commissioner with the Government of India,' 1873. Also 'Indian Annals of Medical Science,' vol. xvi.

[3] 'Richerche intorno alla Bilharzia hæmatobia in relazione colla ematuria endemica dell'Egitto e nota intorno ad un nematoideo trovato nel sangue umano.' Naples, 1874.

Manson[1] of Amoy, and in Australia by Dr. Bancroft[2] of Brisbane. They have also been found in the blood in Brazil; and, within the last few weeks, in England, by Dr. Hoadley Gabb of Hastings.

In considering the possible relation which may exist between the several parasites which have thus been found in different latitudes, it will be well to bear in mind the history of somewhat similar organisms in the circulation of dogs. There is another matter to be taken into consideration as regards the identification of like parasites in man,—namely, their association with diseased conditions. Are these conditions invariably of the same general character in all countries? If so, it would be sufficient to show that a distinct relation of some kind existed between the disease and the parasite; but if it be found, notwithstanding the existence of a general correspondence between them, that nevertheless minor differences were more or less constantly present, this would indicate either that some slight difference existed in the parasite itself or that it bore no causal relation to the disease.

It so happens that the nematoid hæmatozoa are found associated with a disease which, whilst manifesting a close general resemblance in different countries, is nevertheless characterised by a marked difference. In Asia, or at least in India, this disease is known by its most characteristic appearance, viz. milky or chylous urine; whereas in Africa and South America it is described as the "hæmaturia" of various localities, or as "hematurie chyleuse" or "graisseuse," a term doubtless adopted on account of its being a more correct description of the malady than chyluria. In India, however, although the term may be more or less applicable at some period or other of the disease, it is nevertheless not so appropriate, in the great majority of cases, and, indeed, in some instances is wholly inappropriate, as occasionally no marked traces of red colouring matter can be detected in the urine from the beginning to the close of the attack. There is an instance of this kind under my observation at present (a European born in the country) suffering from a third attack, who has never detected the slightest trace of blood at any time. It is of importance that this feature in the character of the disease according to its geographical distribution should be borne in mind, as it may hereafter be found that what at present are generally considered as merely two phases of one malady may each have a distinctive etiology.

[1] "Report on Hæmatozoa," in 'China Customs Medical Reports,' vol. xiii. Shanghai, 1877.

[2] 'On Urinary and Renal Diseases,' by W. Roberts, 3rd Edit., 1876, p. 342.

[3] The 'Lancet,' June 22, 1878, p. 921.

When in March 1870[1] I detected a microscopic nematoid in urine of the latter character, I was under the impression that no nematoid of any kind had previously been found in any urine which could not be attributed to accidental circumstances. It proved, however, that the late Dr. Otto Wucherer had already found a parasite of a like character in 1868 in "*Hæmaturia Braziliensis*," and had forwarded specimens to Prof. Leuckart for identification.[2] Dr. Jules Crevaux succeeded in confirming Wucherer's discovery by finding (27th July, 1870) similar helminths in the urine of a young creole affected with a like disease.[3] It is possible that the parasite discovered by Wucherer and described by him in December, 1868,[4] may prove to be identical with the one found by myself in March, 1870; in such an event it will be necessary to seek forsome clue, other than specific differences in the helminths, to account for the circumstance that the disease with which they are associated presents different characters.

In order to complete the sketch of the history of nematoid urinary parasites of this period it will be necessary to refer to two other observations, as it may be of assistance to future writers in

FIG. 1.—*Trichina cystica:* Embryo of an oviparous nematode, obtained in urine. (Reduced from Dr. Salisbury's figure representing it as magnified 1000 diameters to = × 300 diam.

deciding (1) as to the number of such helminths that may be found in the urine of man, and (2) whether any of them should be considered as pseudo-parasitic merely. In 1868 Dr. Salisbury published an account of a parasite which he had found associated with ova, in the urine of an insane old lady suffering from severe 'cystinic rheumatism;' and affected with partial paralysis of the bladder and of other parts of the body. A drop of urine frequently contained 10 to 15 ova. It was *not* a case either of hæmaturia or chyluria, although it is sometimes erroneously stated that she was suffering from the latter disease. This impression has arisen from the fact of *cystinuria* having been confounded with chyluria, two totally different disorders. The helminth is described as *Trichina cystica* (fig. 1).

[1] "Annual Report of the Sanitary Commissioner with the Government of India," 1870. 'British Medical Journal,' 19th November, 1870.
[2] Leuckart's 'Parasiten,' Band. ii, p. 640.
[3] Idem; and 'Journal de l'Anatomie et de la Physiologie,' t. xi, 1875.
[4] 'Gazeta da Bahia,' December, 1868.

Writing in 1872 Dr. Cobbold, after describing the history of a little girl who had been suffering from hæmaturia associated with the Distomum hæmatobium, refers to the circumstance that he obtained from the patient some other urinary parasites *in the egg condition*.[1] "On five separate occasions," writes Dr. Cobbold, "I obtained one or more specimens of the eggs or embryos of a minute nematode. In one instance there were about fifty of these ova in the urine: their embryonic contents being well developed, and in a state of activity. Usually they were all in this advanced condition; but on the 25th of July, 1870, several were observed in much earlier stages of development." The fully grown eggs gave a longitudinal measurement of $\frac{1}{300}$" by $\frac{1}{1000}$" in breadth. Judging from the description of the ova and their contained embryos, it would seem that the parental form must have been oviparous. The embryos, when freed artificially from the egg, measured $\frac{1}{300}$" in length by $\frac{1}{3500}$" in breadth. On two occasions free dead specimens were observed which had been lying in water some time, and these measured $\frac{1}{130}$" by $\frac{1}{3000}$" The parents of the patient had mentioned that the latter had "passed three small vermiform entozoa by the urethra."[1]

Dr. Cobbold writes: "I have been thus particular in recording these facts, because future discoveries may enable us to identify

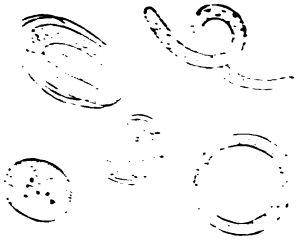


FIG. 9.—Ova and freed embryos of an oviparous nematode; obtained in urine. (After Cobbold.)

the species of nematode to which these ova are referable. I know only one set of observations on record which refer to this same species of parasite." The parasite referred to is the above-cited *Trichina cystica*. As it may be a convenience to future observers to be able to judge of these matters for themselves in the absence of the original papers, I have reproduced Dr. Cobbold's illustrations, together with a reduced outline of Dr. Salisbury's figure. The reduction has been effected by means of a camera lucida, so

[1] During the last seven years I must have examined the sediment of very many gallons of chylous urine, but never observed any ova of nematodes, though, from time to time, I have found many hundreds of embryos.

as to represent the helminth as magnified 300 diameters instead of 1000 as in the original. This will facilitate comparison with Dr. Cobbold's figure representing his nematoid ova parasites[1] (fig. 2). Notwithstanding the discrepancy in size, Dr. Cobbold considers that the helminths are referable to one and the same species. They are both manifestly the offspring of some oviparous nematode; further than that it is, I think, hardly safe to carry the comparison.

The figures will also serve to elucidate another matter, as Dr. Cobbold has since asserted that his parasite is not only identical with Dr. Salisbury's, but also identical with the *Filaria sanguinis hominis*,[2] a figure of which under a somewhat like magnifying power will be found in Pl. XII (figs. 3 and 5). Dr. Douglas Cunningham several years ago pointed out that such a view was untenable;[3] moreover, the mature *Filaria sanguinis hominis* is not oviparous but viviparous.

Changes undergone by the Embryos of Nematoid Hæmatozoa when ingested by the Mosquito.

It would occupy too much space to attempt an epitome of all that has been written regarding the *Filaria sanguinis-hominis* and the somewhat numerous diseases which have been ascribed to its influence, so that for the present the foregoing must suffice. It remains to be considered how it is that the embryos get into the circulation and what becomes of them afterwards. A most important step towards the solution of these queries has recently been made by Dr. Patrick Manson of Amoy.[4] He has shown that, immediately after a mosquito has fed itself on the body of a filaria-affected individual, the insect's stomach will contain living examples of the hæmatozoon; and that the latter will attain considerable progress towards maturity therein, in the course of a few days. It is believed that it then escapes from the mosquito when the latter dies in the water to which it betakes itself, and the filariæ thus find their way into the human body. Dr. Manson's highly interesting paper gives a full account of the various developmental stages, together with figures of the object as they appear from time to time.

I have repeated many of Dr. Manson's experiments and have been able to satisfy myself, from personal observation, that his statements as to what occurs in China may, in most particulars, be made applicable to India also. I had on many occasions ex-

[1] 'British Medical Journal,' July 27, 1872, page 92.
[2] 'London Medical Record,' No. i, vol. i, 1873; the 'Lancet,' July 13, 1878, p. 64.
[3] The 'Lancet,' June 14, 1873, page 835.
[4] 'China Customs Report,' No. xiv, 1878.

amined the stomachs of mosquitoes and of other suctorial insects in a cursory fashion during the last few years, but had never detected parasites resembling the *Filaria sanguinis*. When, however, I learnt of Dr. Manson's success, I proceeded to make examinations in a systematic manner, and found, to my surprise, that 14 per cent. of the insects, caught at random and then examined, contained such embryos.[1] It became, therefore, manifest that filarious blood must be a tolerably common occurrence.

At first I was not successful in being able to detect any but disintegrative changes in the ingested parasite owing to the circumstance that I had carefully restricted the examination to the contents of the stomach only. This was done in order to diminish the risk of confounding the various stages which the embryo-filariæ might undergo with some other parasites which might exist among the tissues of this, as of other insects. The parasites were, in fact, found to be digested. Leuckart[2] mentions that a similar result was observed by Fedschenko to follow the ingestion of Dracunculus-embryos in the stomach of the *Cyclops*. The latter is believed to serve as an intermediary host for the development of the guinea worm, the embryos getting into the body of the Cyclops by piercing the cuticle. When, on the other hand, the embryos are swallowed they are digested.

In the course of the foregoing observations it was observed that all the mosquitoes captured in one of the servants' houses contained hæmatozoa of the same character, and it was found that one of the five persons dwelling in this house harboured filariæ in the blood. The man had been many years in the place and is not known to have suffered from any special disease.

The circumstance that such a constant supply of filarious mosquitoes, of tolerably certain history, was available, materially simplified the course of investigation, which, briefly told, was as follows:

Insects were caught early in the morning in the room in which this person had slept, just as Dr. Manson had done. Some were placed in bell glasses standing in water, others in test-tubes containing a little water at the bottom and covered with a strip of muslin. These were duly labelled and set aside for periodical examination.

When the insect was examined with recently ingested blood in its stomach, it was found that the hæmatozoa, when present, did not differ materially from the aspect presented by them when extracted directly from the blood of its previous host (Pl. XII, fig. 5), although, not unfrequently, parasites would also be seen which

[1] 'Proceedings of the Asiatic Society of Bengal,' March, 1878, p. 89.
[2] Op. cit., Band ii, p. 706.

either belonged to a more advanced stage of the one under consideration, the result of a previous ingestion of filarious blood, or belonged to a totally different kind. There is always, therefore, a risk of confusing different parasites in the same insect. Repeated examinations at the same periods tend, however, to minimise this source of error. During the first twenty-four hours no marked change takes place in the form of the organisms.

On the second day, however, it will probably be seen that the blood has, to a considerable extent, undergone digestion, and the stomach will no longer manifest the distended condition of the first day. Probably a few altered hæmatozoa will be observed in it moving very languidly, presenting the appearance of partially disintegrated fungal filaments when the movements are not manifested. Some of them may be actually dead; these will be found to be stained by eosin solution very readily.

Between the second and the third day further changes occur, but in order to be able to follow these it will be necessary to examine the other tissues of the insect, as possibly the stomach may contain none; it will, however, probably be found that some of them have migrated into the tissues immediately outside this viscus. It will now be observed that some of the parasites have become considerably thicker (fig. 7); and occasionally specimens will be seen with the tail presenting the appearance of a lash (fig. 9); the movements are still very sluggish.

About the fourth day it is probable that examples in various stages of growth will be visible, rendering it extremely difficult or impossible to state precisely what it is that actually does take place; at least hitherto I have not been able to satisfy myself. About this period, however, I have sometimes seen bodies, apparently composed of precisely the same material as figs. 6, 7, 9, undergoing something so very like cleavage (fig. 8) that I hesitate to state that this act is not one of the stages in the development of the filaria. The figure given (No. 8) is very carefully sketched, and, like all the others, accurately to scale. It will be noticed that one end is partially hidden by some granular matter. This I was not able to press away from the preparation. Other preparations of a like kind were also more or less hidden by granular matter, and in some cases (unassociated, however, with any indications of fission) the parasite appeared to be covered with an encrustation. With regard to the process of division suggested by the appearance of No. 8 I can offer no opinion; it is quite possible that it forms a part of the developmental changes undergone by some other parasite,—such, for instance, as a gregarine. About the fourth day there will also be seen short, thick bodies (very appropriately described by Dr.

Manson as "sausage-shaped"), almost perfectly still (fig. 10), with a faint indication of a mouth; and, in some of them, a faint line may be detected suggestive of a commencing intestinal canal; the escape of a few granules on slight pressure towards the other, usually thicker, end, suggests the existence of an anal aperture. The chief difficulty which I have experienced in following these changes is to account for the transition of form at figure 7 to that represented in figure 10. They are all, up to this figure, sketched as magnified by 300.

The larval forms at fig. 10 now rapidly increase in size, and gradually acquire a more elongated outline, and between the fourth and fifth day they may be found presenting the form shown at fig. 11. The last figure, it will be noticed, is magnified 100 diameters only, and the length of the larvæ, therefore, is almost three times that of those delineated at fig. 10. They also manifest greater activity.

The highest stage of development which has come under my notice is that figured at 12 as seen magnified 100 diameters. The anterior and posterior portions of a similar one, magnified 300 diameters, are delineated at fig. 13. This measured $\frac{1}{43}$ of an inch in length, and its width towards the middle was $\frac{1}{60}$; near the anterior and posterior ends they measured $\frac{1}{600}$" across. The dimensions of another specimen which I measured were $\frac{1}{43}$" in length by $\frac{1}{1000}$" in width at the broadest part. Dr. Manson mentions that he has on four occasions observed larger specimens than these.

Notwithstanding their activity and apparently robust condition, they nevertheless are extremely fragile, very slight pressure of the cover-glass being sufficient to crush them. When examined in the unbroken condition it is only with difficulty that the alimentary canal can be distinguised beyond the junction of the œsophagus with the intestine, but when carefully ruptured (as in fig. 12) the tube may be distinguished. I have not been able to distinguish any other differentiated viscus in any of the specimens which have come under my observation, and, certainly, nothing suggestive of differentiation of sex.

By the time that the larval filariæ have attained to this degree of development, the mosquito will possibly have already deposited its ova and its own cycle will have been nearly completed. With the intention of following out the development still further, I have frequently kept insects until this stage was reached before examination, but all the attempts have proved fruitless, notwithstanding that the mosquito has been seen to go through its ordinary course of depositing its ova on the surface of water, and then perishing itself. Either no filariæ were found in its body, or if present they were dead, and careful examination of the

water invariably yielded negative results in my hands. It would seem that the larvæ had perished. As the quantity of water used was so small, it is hardly possible, had filariæ in any stage of growth been present, that they could have so completely escaped observation. Possibly the more or less artificial conditions necessarily associated with the conduct of such experiments may account for these negative results. In the meantime I cannot, as a result of personal observation, affirm that a sojourn in the body of the mosquito, and subsequent transference to water, suffice to bring the *Filaria sanguinis-hominis* to maturity.

A few words may be said regarding other hæmatozoic parasites which appear to find their way into the bodies of mosquitoes. In the first place, it may be mentioned that *dogs* appear to furnish a certain proportion, as I have repeatedly found Filariæ in these insects in which not the slightest trace of the enveloping cyst, which characterises the human hæmatozoon, could be detected. Unfortunately the corpuscles of the dog's blood are so like those of man, as to size and appearance, that it is not possible to distinguish them with certainty, so that the examination of the fluid contents of the mosquito's stomach does not tend to throw any light on the source of the hæmatozoa in this instance. It is probable that other animals also contribute towards rendering the diagnosis more difficult.

FIG. 3 . . . . × 500 diam.
Embryos of a nematoid helminth from a bird, obtained in the stomach of a mosquito. A few blood-corpuscles are included in the sketch.

It is not uncommon, for example, to find the blood-corpuscles of *birds* forming a portion of the contents of the mosquito's stomach, and I have on several occasions observed extremely small embryo-nematodes associated with such corpuscles. Some of these are represented in the accompanying woodcut (fig. 3). If these helminths be compared with the figure given of the

hæmatozoon of the crow,[1] they will be found to bear a close resemblance to it. It is very possible that these embryos may not have been derived from the crow, but there can be but little doubt, judging from the character of the red blood-corpuscles, that they had been derived from some bird. Facts of this kind also add to the difficulty of ascertaining precisely the various developmental processes which any particular species of hæmatozoon undergo.

The Mature form of Filaria sanguinis-hominis.

A letter appeared in the 'Lancet' of 14th July, 1877, from Dr. Cobbold, announcing the discovery of Dr. Bancroft, of Brisbane, Australia, of what was believed to be the mature *Filaria sanguinis*. They had been found on two occasions; on the first, a dead specimen was found in a lymphatic abscess of the arm; and the second time four living specimens were obtained whilst tapping a hydrocele of the spermatic cord. Regarding these Dr. Bancroft had written the following description: "The worm is about the thickness of a human hair, and is from three to four inches long. By two loops from the centre of the body it emits the filariæ described by Carter in immense numbers."

During the last six years I have taken considerable interest in questions of this nature, and have, through the kindness of professional friends in India, had frequent opportunities of searching for the parental form of the *Filaria sanguinis-hominis*, but only succeeded in obtaining it on one occasion. This was a little more than a year ago—7th August, 1877. Descriptions of the specimens were published at the time,[2] but, in a paper dealing with the organisms of the blood, a brief account of these particulars should find a place.

For the opportunity of examining the particular case in which the filariæ were found I am indebted to the kindness of the late Dr. Gayer. The patient was a young Bengalee affected with well-marked nævoid elephantiasis of the scrotum, associated with the presence of embryo-filariæ in the blood. The tumour and the sanguineous exudation which escaped on its removal were collected, and submitted to careful examination, and, after a continuous search of eight hours, the long sought-for helminth was eventually obtained. The specimens were, however, so greatly mangled by the needles used in teasing a clot under a dissecting

[1] We hope to be able to reproduce the section of the monograph dealing with the microscopic hæmatozoa of animals in our next number.—Ed.

[2] 'Indian Medical Gazette, 1st September, 1877; 'The Lancet,' 29th September, 1877, p. 453; 'Centralblatt für die medicinische Wissenschaften,' No. 43; 1877, p. 770.

microscope, that the description of parental forms cannot at present be so complete as desired.

The specimens consisted of portions of two worms, male and female (Plate XII, figs. 1 to 4); the former, however, had unfortunately been torn across at two places, and the terminal ends could not be discovered. Both specimens manifested very lively movements, notwithstanding their mangled condition. They were of a white colour, the cuticle was smooth and devoid of transverse markings, except such as were due to the contraction of the subjacent muscular walls.

The fragment of the male specimen which was found measured half an inch in length, and $\frac{1}{160}$ of an inch (·14 mm.) transversely; it was thinner than the female, but of considerably firmer texture—so firm, indeed, that whilst endeavouring to make out its anatomy a considerable portion of it was lost by one of the needles used for dissecting snapping, and carrying a portion of worm along with it. On tearing the helminth across, the severed surface does not present a ragged edge, but an even outline (Pl. XII, fig. 4). The male manifested also a great tendency to coil, and it was only with difficulty that it could be separated from the specimen of the female parasite, around a portion of which it had twisted itself. It is unfortunate that its caudal end especially could not be found, as the definite decision of the genus to which it should be referred depends in a great measure on the characters which the posterior end of the male worm presents. The intestinal canal measured $\frac{1}{630}''$ (·039 mm.) across, and the sperm tube $\frac{1}{1500}''$ (·016 mm.).

The caudal end of the female worm also had been severed, and could not be found; this, however, is of less moment. The length of the portion of the helminth secured was 1¼ inch, and its greatest width about $\frac{1}{160}$ inch. It was packed with ova and embryos in various stages of development; the latter, especially those of them which were mature, manifested active movements. The head is slightly club-shaped; the mouth does not manifest any very distinctly marked labial subdivisions, nor are there any chitinous processes evident, either before or after death. The œsophagus is faintly striated, and shades off imperceptibly into the intestinal tube, the latter being filled with moleculo-granular matter.

The following measurements may be useful to future observers:

Oral aperture to end of œsophagus . .	$\frac{1}{55}$	of an inch, or	·45 mm.
Diameter of oral aperture	$\frac{1}{3000}$	„	„ ·008 „
Width of extreme end (anterior) . .	$\frac{1}{517}$	„	„ ·047 „
Ditto anterior end at "neck" . .	$\frac{1}{648}$	„	„ ·045 „
Ditto opposite junction of intestine with œsophagus	$\frac{1}{233}$	„	„ ·112 „
Ditto about ¼ inch from anterior end .	$\frac{1}{158}$	„	„ ·162 „
Width where packed with ova and embryos	$\frac{1}{100}$	„	„ ·25 „
Width of uterine tube filled with ova .	$\frac{1}{233}$	„	„ ·112 „
Ditto alimentary tube . . .	$\frac{1}{686}$	„	„ ·037 „

The ova do not possess any distinctly marked "shell;" from the smallest to the largest nothing but a delicate pellicle can be distinguished as enveloping the embryo in all its stages; consequently the form assumed by the ovum depends to a great extent on the degree of the surrounding pressure. In fig. 3 (Plate XII) ova of various shapes are depicted (spherical, triangular, oval), and with a considerable latitude as to size. The average of six measurements of the less advanced kinds of ova, *i. e.* those in which the outline of the embryo was not distinctly evident $= \frac{1}{139}''$ (·018 mm.) by $\frac{1}{2000}''$ (·012 mm.); whilst the average measurements of three ova in which the embryos were visible $= \frac{1}{686}''$ (·037 mm.) by $\frac{1}{790}''$ (·030 mm.).

When the latter, after having arrived at this stage of development, are examined during life, it is in many instances difficult to state whether they are to be considered as freed embryos or not, as the "egg-shell" has become so extremely attenuated and translucent as only with difficulty to be distinguished. By pressing the covering glass firmly the sac may often be ruptured. It, however, appears probable that, even when the embryo acquires worm-like appearances, the envelope is not lost in this species so long as it continues in the blood.

It is of importance to bear this in mind, as, contrary to what is seen with regard to the nematoid hæmatozoa of dogs, the embryos in the blood of man are each contained in a translucent cœcal tube. This tube is readily recognisable during life whenever the embryos can be properly observed in fresh clear serum, as also in spirit-preserved preparations. I possess at the present time specimens thus preserved of both species, one being contained in blood removed from the heart of a person, who during life, was known to harbour hæmatozoa, and the other obtained from the blood-vessels of a dog similarly affected. In not a single instance have I been able to distinguish the least trace of an enveloping tube in the latter, whereas in the former this tube can be clearly demonstrated in the majority of instances. Hence, notwithstanding their almost complete accord as to dimensions, the character just referred to is sufficient to distinguish slides prepared from either of these two specimens. A like distinction

has been ascertained to exist between the two kinds of embryo filariæ in China by Dr. Manson; but, according to Dr. Sonsino, those of Egypt, and apparently those of the Brazils, do not present this distinguishing feature. As may be recollected it was mentioned that a distinction also exists between the disease with which the human hæmatozoon is associated in the different countries—not a great difference certainly, but, nevertheless, one which should be borne in mind when deciding as to specific distinctions between the parasites.

It must also not be forgotten that the inhabitants of Brazil and of certain parts of Africa are, as has been known for at least a century, peculiarly liable to be the hosts of tissue-parasites. The minute thread-like sub-conjunctival filaria (*Filaria loa*), for example, though from two to six inches in length, has never been accurately described, and its precise thickness is not known yet, although it was discovered by Bajon so long ago as 1768,[1] and has since been frequently observed beneath the skin and conjunctiva of negroes and other persons. M. Guyon brought it before the notice of the French Academy in 1838, and again in 1864. On the former occasion, the specimens measured 30—40 mm., but the helminth described in 1864 was 150 mm., in length. It is not quite clear that they belonged to the same species. It is not impossible that the embryos discovered by Dr. O'Neill[2] in a disease of the skin termed *Craw-craw*, on the west coast of Africa, may prove to have been the offspring of some such helminth.

Again, the minute, thread-like nematoid described in America by Leidy, five inches in length and $\frac{1}{60}$ inch in greatest breadth, is not to be overlooked. It was obtained from the mouth of a child, and derives its name—*Filaria hominis oris*[3]—from this circumstance.

All these circumstances point to the necessity of exercising considerable caution in arriving at any decision as to the precise relation of any of these as yet obscure parasites.

With regard to the helminths discovered by Dr. Bancroft in Australia, I am not in a position to offer an opinion. It has not yet been shown that they are blood-worms in the ordinary sense of the term, nor is it known that the individual from whom they were obtained harboured embryo hæmatozoa. It is further to be remarked that the affections under which the persons laboured from which they were derived were not of the character of the diseases with which these hæmatozoa have hitherto been known to

[1] 'Comptes Rendus,' t. lix, 1864, p. 745.
[2] 'The Lancet,' Feb. 10, 1875, p. 265.
[3] 'Proceedings of the Academy of Natural Science,' Philadelphia, vol. v, 1850-51.

be associated; indeed, it would appear that one of the principal morbid conditions with which they are associated in this country —nævoid elephantiasis—is unknown in Australia. It may also be noteworthy that no male worm was found among the specimens.

Dr. Cobbold is, however, of opinion that they are identical, and it would be superfluous to say that the opinion of one who has devoted so many years to the study of helminths is entitled to consideration. This observer has lately (the 'Lancet,' July 13, 1878) given a summary of the bibliography, &c., of these questions, in which I observe a slight error. It is with reference to the mature nematoid helminths found in Australia. These, Dr. Cobbold states, were "first discovered by Dr. Bancroft and first described by myself." It seems to me, however, that not only did Dr. Bancroft discover the parasite, but also furnished the first account of them which appeared. It is possible that the description supplied by Dr. Bancroft, which is quoted on a previous page, is not considered sufficiently precise to be accepted as such, from a naturalist's point of view. Allowing this, if, as Dr. Cobbold maintains, the Australian and Indian parasites are identical, the first full account of the mature *Filaria sanguinis hominis*, as found in India, was published, both in this country and in London, previous to the appearance of Dr. Cobbold's description—having, indeed, been in the printer's hands before Dr. Cobbold had even seen the Australian parasites. Dr. Cobbold, moreover, refers to such prior publication in the appendix to his own article.

This trifling oversight will, I have no doubt, be duly corrected should this distinguished observer have occasion to write regarding these subjects in the future.

In considering the question of the relation which may exist between the presence of organisms in the circulation and disease, the conclusion is forced upon us that in reality but little of a definite character is known. One thing, however, is clearly manifest, that the supposition that beings become asphyxiated as a result of the existence of living organisms in the blood, is untenable. The study of their natural history as they occur in man or animals does not afford the slightest support to such a view. Indeed, so far as we at present know, it would seem that the presence of embryos in the blood, no matter how numerous, exercises no marked deleterious effect on the organism. It is probable, however, that the parents of these organisms, especially when helminthic, do exert a deleterious influence on the well-being of their hosts,—as, for example, the lesions which exist in the walls of the blood-vessels caused by the *Filaria sanguinolenta*, would seem to indicate. With regard to allied conditions in man, it is to be inferred that the influence exerted by nematoid

embryos in inducing disease is apt to be overrated, as it would seem that the parasites may sojourn for long periods in the system without inflicting obvious injury. That certain injuries are effected, however, cannot well be doubted, but, judging from what we know of the like condition in animals, the injuries result, not from direct action of living organisms on the blood current in which they dwell, but from their action on some of the delicate tissues through which the blood circulates—such injurious influence being probably exerted, more especially during the migrations of the parents of future embryo-hæmatozoa.

CALCUTTA;
August, 1878.

MEMOIRS.

Notes *on some of the* Reticularian Rhizopoda *of the* "Challenger" Expedition. By Henry B. Brady, F.R.S. With Plate VIII.

II.—*Additions to the knowledge of Porcellanous and Hyaline types.*

In a former paper ('Quart. Journ.' for January) a brief notice was given of a few of the more interesting types of Arenaceous Rhizopoda occurring in the dredged stuff brought home by Sir C. Wyville Thomson and the scientific staff of the "Challenger" Expedition, and I propose now to describe a limited number of forms pertaining to other groups of the Foraminifera, concerning which fresh facts have been gathered, tending to elucidate the natural history of the order.

Porcellanea.

In no section of the subject has so little that is new been elicited from the "Challenger" results as in the Family Miliolida of Carpenter, Parker, and Jones. Abundance of large *Biloculinæ* and the like are of course to be found in the *Globigerina*-ooze of deep-sea bottoms, and there is considerable variety in the forms furnished by some of the shallower dredgings from the tropics, but there is no such range of well-marked modifications of the common types as one would be pretty sure to meet with, for example, in material from depths of five to fifty fathoms in the Red Sea; and as few or no shore-sands were collected during the expedition, there is a comparative absence of even the common littoral species. The Miliolida are to be regarded as essentially a shallow-water and littoral group. It is true that the very largest examples of certain genera are found amongst the *Globigerina*-mud of 1000 to 2000 fathoms, or even at greater depths, but the species so occurring are very limited in number, and the specimens as a rule comparatively few, whilst in shallow water and in shore-sands even the deep-sea species, with one or two exceptions, are common, though the in-

connection with the genera *Nubecularia* and *Dactylopora* will be alluded to presently in the notice of two species, *N. tibia* and *D. eruca*. Concerning the spiral types there is, perhaps, even less that calls for remark. The genera *Peneropolis*, *Orbiculina*, *Orbitolites*, and *Alveolina*, are all well represented in the "Challenger" gatherings, but the results of their examination tend rather to diminish than to increase the number of forms to be recognised as "species."

NUBECULARIA TIBIA, *Jones* and *Parker*, Pl. VIII, figs. 1, 2.

Nubecularia tibia, Jones and Parker, 1860. 'Quart. Journ. Geol. Soc.,' vol. xvi, p. 455, p. 20, figs. 48—51.

The interest attaching to this simple little organism depends upon the fact that until recently it has only been recognised as a Triassic or Rhætic fossil. It was described by Messrs. Jones and Parker, *loc. cit.*, in their paper upon the Foraminifera of certain marls from Chellaston in Derbyshire. Within the last few months I have identified specimens in Mr. E. A. Walford's collection of microzoa from the Upper Lias of Banbury, and this completes the record of its geological history; it is, nevertheless, quite possible that, owing to its minute size and inconspicuous appearance, it may have been overlooked in other habitats. A careful comparison of specimens from all the known sources, recent and fossil, reveals no characters not common to the whole of them, none at any rate that can be regarded as zoologically distinctive.

Nubecularia tibia occurs at two of the "Challenger" stations, both in comparatively shallow water, namely, amongst the Philippine Islands (95 fathoms), and in Humboldt Bay, Papua (37 fathoms).

DACTYLOPORA ERUCA, *Parker and Jones*. Pl. VIII, figs. 3, 4.

Dactylopora eruca, Parker and Jones, 1860. 'Ann. and Mag. Nat. Hist.,' ser. 3, vol. v, p. 473; Carpenter, 1862, 'Introd.,' p. 128, pl. 10, figs. 1—8.

Haploporella eruca, Gümbul, 1872. 'Abhandl. der k. bayer. Akad. der W.,' II Cl., vol. xi, p. 256, pl. D. 1, fig. 1.

Decaisnella eruca, Munier-Chalmas, 1877. 'Comptes Rendus de l'Acad. des Sci.,' vol. lxxxv, p. 816.

I do not propose to enter here upon the controversy concerning the true nature and position of the *Dactyloporidæ*,

but as *Dactylopora eruca* occurs in considerable variety of form in some of the parcels of material which I have examined it can scarcely be passed over without notice.

The latest contribution to the debate is a brief note by M. Munier-Chalmas (*loc. cit.*), in which *Dactylopora* and all it allies, including *Acicularia*, are assigned to a family of calcareous Algæ, characterised as "*Siphonée verticillée.*" It may be confessed that the multiform organisms hitherto associated under the term *Dactyloporidæ* have constituted an anomalous and unsatisfactory group, and any fresh light on their structure and relationship will be welcomed by systematists, whether zoologists or botanists. It is not at all improbable that beings of widely different affinities have been placed together for want of accurate knowledge; but if this be the case, to hand them in mass to another position will not mend matters greatly.

It is difficult to see how irregularly constructed shells, like those represented in Pl. VIII, figs. 3, 4, can have formed portions of a radiate or verticillate organism; nor have I, after the examination, by sections and otherwise, of a large number of fresh specimens of *D. eruca*, seen anything corresponding to the structures figured in M. Munier-Chalmas' paper. Nevertheless, as we have only the author's preliminary note, criticism would be premature, and we must await the publication of the promised detailed memoir. Meanwhile, it may be observed that the characters of *Dactylopora eruca* are easily reconciled with those of the rest of the Miliolida, and, so far as revealed by the dead shells, present no anomaly in the position in which the species has been placed by Messrs. Parker and Jones.

Of the new Milioline forms alluded to in the foregoing paragraphs, the following will serve as descriptions, pending the publication of more detailed notice with the necessary figures.

Hauerina exigua, *n. sp.*

Characters.—Test free, thin, discoidal, planospiral; composed of a number of convolutions of a narrow, slightly embracing, septate tube, but showing no indication of the spiral suture beyond the final circuit. Septa few, about three in each convolution, not marked by any external depression. Aperture simple, terminal. Diameter $\frac{1}{50}$ inch (0·5 millim.) or less.

Found in shallow water in the tropics, notably about the Admiralty Islands and New Guinea. This species also occurs in the Red Sea and elsewhere.

HAUERINA INCONSTANS, *n. sp.*

Characters.—Test free, thin, commencing growth as a planospiral, non-septate tube, after a time becoming spiroloculine in arrangement, and eventually forming convolutions, each consisting of several (two, three, or four) irregularly arcuate or sigmoid segments. Periphery bordered by a broad thin wing, seldom found entire. Diameter of large specimens, $\frac{1}{15}$ inch (1·6 millim.).

Hauerina inconstans is widely *distributed*, geographically speaking, but the total number of specimens found is very small. In the "Challenger" dredgings it occurs at depths varying from 210 to 2300 fathoms.

MILIOLINA TRIQUETRA, *n. sp.*

Characters.—Test free, compressed, subtriangular; composed of few segments, of which three, arranged on one plan, usually go to form each of the later convolutions. Aperture simple, situate on the produced neck-like extension of the terminal segment. Texture roughly arenaceous externally. Diameter $\frac{1}{25}$ inch (1· millim.)

A rare species, the best specimens of which are from anchor-mud in Humboldt Bay, Papua, 37 fathoms.

MILIOLINA ALVEOLINIFORMIS, *n. sp.*

Characters.—Test free, elongate, fusiform; composed of narrow chambers arranged more or less spirally around the long axis. Segments numerous, sometimes seven or eight visible on the exterior; ventricose or subcylindrical, arcuate. Aperture porous or radiate, obscure, terminal. Texture thin, porcellanous and nearly smooth in very young shells; finely arenaceous in adult specimens. Length $\frac{1}{10}$ inch (2·5 millim.) or more.

Not unfrequently met with in the shallow waters and shore-sands of tropical latitudes.

Hyaline or Vitreous Types.

Of the three families which constitute the Suborder PERFORATA of Carpenter, Parker, and Jones, namely, *Lagenida*, *Globigerinida*, and *Nummulinida*, the last named may be dismissed in a word. The "Challenger" spoils

have, in fact, added little or nothing to our knowledge of the *Nummulinida*, except in so far as concerns their geographical and bathymetrical distribution.

Lagenida.

Amongst the *Lagenida* it is far otherwise. The genus *Lagena* alone, as represented in these collections, supplies material for five or six crowded quarto plates, its varieties embracing modifications of contour and of surface decoration of which little was previously known. Of these it is impossible to speak with any advantage in the absence of figures. It has been generally understood heretofore that the central home of the *Lagenæ* was in water of 100 to 200 fathoms, but some of the most beautiful and delicate members of the genus have been found at depths of 2000 to 3000 fathoms, and even in the black mud of almost the deepest of the ocean abysses hitherto explored by the dredge; and in some of these localities the variety of the forms which have been met with has been scarcely less remarkable than their individual beauty.

Amongst the Nodosarine types furnished by the "Challenger" dredgings the most noteworthy is the genus *Frondicularia*, which, with its subordinate Flabelline modifications, must now take a definite position in the category of recent genera. D'Orbigny, in his 'Tableau Méthodique,' 1826, mentions "the Adriatic" as the habitat of *Frondicularia alata* and *Fr. rhomboidalis*, but it has been supposed by subsequent observers that his specimens were interlopers which had been washed out of one or other of the fossiliferous Tertiary clays that abound in the Italian Peninsula. Messrs. Parker and Jones,[1] however, found the closely allied *Fr. complanata* in dredgings made by the late Mr. Lucas Barrett off the coast of Jamaica (100 to 200 fathoms), and as I have since identified the same species in beautifully fresh-looking specimens collected by my friend Dr. Tiberi, of Portici, on the coast of Sicily, it may be allowed that d'Orbigny's habitat is probably correct. My friend M. Ernest Vanden Broeck[2] reports the occurrence of varieties of both *Fr. complanata* and *Fr. alata* in one of the soundings made by the late Professor Agassiz off Barbadoes, in 100 fathoms. This completes the record, so far as I know, of observations upon recent *Frondiculariæ*, and it is confined,

[1] 'Report Brit. Assoc.,' 1863. Trans. sections, pp. 80 and 105.

[2] 'Ann. Soc. Belge de Micros.,' vol. ii, p. 109, pl. 2, figs. 12—14, and pl. 3, fig. 2.

as will be seen, to three species. But the series that has been collected from the "Challenger" dredgings much enlarges the area of our knowledge. Not only have two of the forms which have been alluded to, together with their Flabelline modifications, been found, but in addition a number of other smaller species of widely different contour, some of which are described and figured in the present paper.

The little branching organism, named *Ramulina* by Professor T. Rupert Jones, hitherto only known by worn fragments occurring amongst fossil microzoa of Cretaceous age, has been found in sufficient numbers, and, notwithstanding its fragile nature, sufficiently complete in all its parts to yield accurate data as to its zoological characters.

The genus *Uvigerina* has also received considerable accessions, and the connection, suggested by Messrs. Parker and Jones, between the normal spiral varieties and the dimorphous shells constituting d'Orbigny's genus *Sagrina*, is confirmed and illustrated by certain new and interesting modifications of the typical structure. A notice of some of these will be found on a subsequent page.

Genus—FRONDICULARIA, *d'Orbigny*.

FRONDICULARIA SPATHULATA, n. sp. Pl. VIII, fig. 5 *a. b.*

Characters.—Test long, narrow, tapering, compressed; margin rounded, somewhat lobulate; sutures but slightly excavated. Primordial chamber inflated; early segments more bent than the latter ones. Surface smooth. Length $\frac{1}{25}$ inch (1·0 millim.).

This is one of the narrow compressed Nodosarian shells that might with almost equal propriety be placed either with *Lingulina* or *Frondicularia*, the slightly inflated primordial chamber and bent earlier segments suggesting the latter genus for preference. Terquem figures a somewhat similar form as *Frondicularia sacculus* ('Sixième Mém. sur les Foram. du Lias,' p. 482, pl, 19, fig. 20 *a. b.*) and the *Fr. linearis* of Philippi ('Beitr. zur Kennt. d. Tert-Verstein,' p. 5, pl. 1, fig. 32) is a Flabelline variety, with analogous general contour.

Such varieties are very rare in the living condition, and there is only a single habitat to record for that now described, namely, off the Ki Islands, 129 fathoms.

FRONDICULARIA COMPTA, *n. sp.* Pl. VIII, fig. 6.

Characters.—Test long, spathulate; truncate or emarginate at the base, obtuse-angular at the apex; margin square, somewhat lobulate. Early segments larger than the later ones, sutural lines limbate. Surface otherwise smooth. Length $\frac{1}{25}$ inch (1·0 millim.).

A very beautiful little shell, with just sufficient irregularity in conformation to make it difficult alike to describe in well-defined terms or to reconcile with previously recorded species. The earlier portion of the test is built on a bolder, larger plan than the latter part, and the septal lines are thickened and raised. The later segments are narrower and smaller, and the sutures, though still limbate, are not so prominent. The peripheral margin is nearly square.

The figured specimen was found at Station 162, Bass Strait, 38 fathoms.

Genus—FLABELLINA, *d'Orbigny.*

FLABELLINA CUNEATA (*von Münster*). Pl. VIII, fig. 7.

Frondicularia cuneata, Von Münster,[1] 1838. 'Neues Jahrbuch für Min.,' 1838, p. 383, pl. 3, fig. 10.

Notwithstanding the more regular contour of the recent specimen and its somewhat larger number of segments, there is no real impropriety in identifying it with Von Münster's species; less impropriety, at any rate, than adding a fresh name to an already over-named genus, on insufficient grounds. Our recent shell, like Von Münster's figure, is long, narrow, and tapering to a point at the base. The early segments are set obliquely and rather irregularly; there is no external limbation or thickening of the sutural lines, and the surface is traversed by delicate, nearly parallel, longitudinal striæ or riblets. The length of the specimen, which is not quite perfect, is about $\frac{1}{25}$ inch (1·0 millim.).

Habitat.—off the Ki Islands, 129 fathoms.

FLABELLINA FOLIACEA, *n. sp.* Pl. VIII, figs. 8—10.

Characters.—Test depressed, complanate; peripheral contour variable, often more or less carinate. Chambers slightly inflated. Spiral segments irregular; equitant

[1] In F. A. Roemer's paper, "Die Cephalopoden des Nord-Deutschen tertiären Meersandes."

segments reaching far towards the base of the test; in some specimens each chamber completely encloses the lateral margins of the preceding one. Sutures excavated. Shell-wall delicately thin; surface smooth. Length $\frac{1}{25}$ inch (1·0 millim.).

Dr. Conrad Schwager, in his beautifully illustrated memoir on Fossil Foraminifera from Kar Nikobar,[1] describes and figures, under the name *Frondicularia foliacea*, a species having characters quite analogous to those of many of the recent specimens, with the exception that, whilst the fossil form appears to be symmetrical (Frondicularian) in its mode of growth, the still-living shells are all dimorphous, that is to say either irregular or Cristellarian, in the arrangement of their earlier segments. Some of the broader, complanate, recent specimens can scarcely be distinguished from Schwager's species. Dimorphous growth is probably an indication of depauperating influences; hence it seems better to retain the term *Flabellina* as distinct from *Frondicularia*, otherwise I should see no reason for separating the recent from the fossil form.

Flabellina foliacea occurs at two stations near the Ki Islands (129 faths. and 580 faths.), in one sounding off the coast of New Zealand (275 faths.), and in one locality off the Eastern coast of North America (1240 faths.).

Genus—RAMULINA, *Rupert Jones.*

RAMULINA GLOBULIFERA, *n. sp.* Pl. VIII, figs. 32, 33.

Characters.—Test free, branching, composed of segments of different sizes connected by stoloniferous tubes. Segments numerous (two to eight or more), globular or subglobular, each with several (two to six) tubulated apertures extended from different portions of the periphery, some of which terminate in fresh chambers. Stoloniferous tubes narrow, circular in section, about equal in length to the diameter of the larger chambers. Texture hyaline; surface hispid or aculeate. Length, when complete, $\frac{1}{15}$ inch (1·7 millim.) or more.

In Mr. Joseph Wright's 'List of the Cretaceous Microzoa of the North of Ireland'[2] there appear figures of two obscure organisms under the generic name *Ramulina*, given to them by Professor T. Rupert Jones. The specimens from which

[1] 'Novara-Exped., Geol. Theil.,' vol. ii, p. 236, pl. 6, fig. 76.

[2] 'Report and Proc. Belfast Nat. Field Club,' 1873-4; Appendix, p. 88, pl. 3, figs. 19, 20.

these figures are taken are probably merely fragments, and no description of genus or species is given beyond that conveyed in the terms "simple, calcareous, subsegmented, branching, Nodosarian form." The diagnosis is further complicated by the author referring to the same genus, "the so-called *Dentalina* (?) *aculeata*" of the Chalk. D'Orbigny's *Dentalina aculeata*, as far as I can gather from the original description and figure,[1] is a characteristic and easily recognised true *Dentalina*, and why it should be associated with any "Ramuline" form it is difficult to understand. Having for some time past been collecting materials for the study of the Cretaceous types of Foraminifera I have become quite familiar with the organisms figured by Mr. Wright, and I believe them to be closely allied to the recent species above described. I have, therefore, adopted the generic term proposed by Professor T. Rupert Jones, and must leave the determination of the distinctive characters of the recent and fossil species until better specimens of the Cretaceous forms can be found to serve as a basis for their more accurate treatment.

The test of *Ramulina globulifera* is always hyaline and perforate, and usually more or less hispid. The genus is probably nearly related to the *Nodosarinæ*, as suggested in the foregoing quotation, but its branching habit of growth is an essential and distinctive feature.

The "Challenger" dredgings have yielded examples from at least nine or ten stations. These are, for the most part, at no great distance from island groups, either in the North Atlantic or in the South Pacific; the depth of water ranging from 145 to 600 fathoms, and the bottom commonly consisting of coral *debris* or shelly sand.

Genus—UVIGERINA, *d'Orbigny*.

The specimens from the "Challenger" collections representing the genus *Uvigerina* form an exceedingly interesting series, and there is one group in particular, namely, that embracing the dimorphous varieties, on which considerable new light is thrown by them. The general characters of *Uvigerina* (proper) are well understood, but this is far from being the case with the forms assigned to the genus or subgenus *Sagrina*.

Normally, *Uvigerina* may be described as having an elongated spiral test, the clustering chambers of which are

[1] 'Mém. Soc. Geol. Fr.,' 1840, vol. iv, p. 13, pl. 1, figs. 2, 3.

arranged with more or less regularity on a triserial plan. The aperture is simple, and usually situated on a produced neck of some sort, either a mere rounded conical projection or, more characteristically, in a tube of greater or less length, terminated by a phial-like lip. The surface of the test is almost invariably ornamented by striæ or costæ (continuous or interrupted), spines, bristles, or other exostoses.

It is, however, on certain divergences from this typical plan of growth, which elucidate the connection ofthe extreme modifications of *Sagrina* with the generic type, that the chief interest of the forms to be described depends.

UVIGERINA PORRECTA, *n. sp.* Pl. VIII, figs. 15, 16.

Characters.—Test elongate, subspiral; earlier segments compactly arranged, obscurely triserial; later segments uniserial, alternating irregularly, more or less distinct and interrupted. Surface marked by delicate, irregular, longitudinal costæ. Aperture produced, tubular. Length $\frac{1}{50}$ inch (0·5 millim.).

Habitat.—Off Bermuda, 435 fathoms; off Papua, 155 fathoms; and at a point about 10° north of the Equator, in nearly the same longitude as the latter, 1850 fathoms.

UVIGERINA INTERRUPTA, *n. sp.* Pl. VIII, figs. 17, 18.

Characters.—Test elongate, subspiral, composed of a number of inflated or subglobose segments, gradually increasing in size, arranged around a long axis. Earlier segments combined so as to form a compact spire; the one or two last formed placed independently, in single irregular series, terminating in a tubular neck. Surface hispid or aculeate. Length $\frac{1}{50}$ inch (0·5 millim).

Habitat.—Humboldt Bay, Papua, 37 fathoms.

Genus—SAGRINA, *d'Orbigny.*

The range of morphological variation in *Uvigerina* runs nearly parallel to that of *Textularia*. The latter genus, which is normally biserial, has subtypical modifications which, on the one hand, may be uniformly triserial, or on the other, may run into uniserial forms; or, taking a dimorphous character, may be spiral, triserial, or biserial in their early stages, and biserial or uniserial in their later growth.

Uvigerina has normally a spiral arrangement of its chambers, but in like manner runs into dimorphous forms, and

these constitute d'Orbigny's genus *Sagrina*. They have been much misunderstood, and have been placed by German systematists, without exception, in the same family with *Textularia*. Of the two species named by d'Orbigny, one[1] is biserial, and only betrays its affinity to *Uvigerina* by its aperture, which is placed in an erect mammillate protuberance at the top of the terminal chamber; the other is a Cretaceous species[2] with an arenaceous test, which is spiral in its earlier growth and finishes biserially. Continental Rhizopodists have only recognised the latter of these, and *Sagrina* has consequently been spoken of as an exclusively fossil genus, with characters founded on those of *S. rugosa*. Messrs. Parker and Jones, however, have shown the relationship which exists between these and some similar forms, and have described two recent dimorphous species,[3] in both of which the arrangement of the segments is partly alternate or triserial and partly uniserial. To these the "Challenger" material has brought two additional and even more abnormal varieties, which have been named *Sagrina virgula* and *S. divaricata* respectively.

The generic term is written *Sagraina* by Reuss and by Zittel. There is no doubt that d'Orbigny named the genus in honour of De la Sagra, the historian of Cuba, but his particular method of doing so does not concern us, and as it is quite clear that the final *a* was dropped intentionally, we must take the genus as he left it. It is the old story of *Textularia* and *Textilaria*, of *Orbitolites* and *Orbitulites*; the only chance of uniformity in nomenclature lies in the rule of precedence. The systematic names for which classical authority and exactitude can be claimed are few indeed.

SAGRINA VIRGULA, *n. sp.*, Pl. VIII, figs. 19—21.

Characters.—Test linear, straight or curved, cylindrical, tapering, composed of many segments. Early segments minute, clustering, obscurely spiral, sometimes wanting; later ones subglobular, united end to end, and somewhat embracing. Aperture wide, with a turned-over phial-like lip. Surface hispid or setose. Length, $\frac{1}{30}$ inch (0·5 millim.).

The relationship of *S. virgula* with the hispid varieties of *Uvigerina* may be seen by comparing the figures with those of *U. interrupta* immediately preceding them in the plate.

[1] *Sagrina pulchella*, 'Foram. Cuba,' p. 140, pl. 1, figs. 23, 24.

[2] *Sagrina rugosa*, 'Mém. Soc. Geol. Fr.,' vol. iv, p. 47, pl. 4, figs. 31, 32.

[3] *Sagrina raphanus* and *S. dimorpha*, 'Phil. Trans.,' vol. clv, p. 364, pl. 18, figs. 16—18.

It is a rare form, and individuals like that represented by fig. 21 may easily be mistaken for minute *Nodosariæ*.

Specimens of this species have been found at three localities in the Eastern Archipelago, all in shallow water (15 to 37 fathoms) and in one deeper sounding on the coast of South America, off Pernambuco (675 fathoms).

SAGRINA DIVARICATA, *n. sp.*, Pl. VIII, figs. 22—24.

Characters.—Test free, moniliform; spiral chambers few and minute, forming an obscure rounded mass, altogether but little larger than one of the later segments. Later segments two to four in number, subglobular, arenaceous externally, united by clear, non-arenaceous, stoloniferous tubes, of length equal to about half the diameter of the larger chambers. Aperture an elongate, tubular neck, often longitudinally furrowed, and with an irregular, expanded lip. Length, $\frac{1}{50}$ inch (0·5 millim.).

The occurrence of arenaceous modifications of the dimorphous *Uvigerinæ* is quite in harmony with the parallelism that has been suggested between them and the Textularian series. One species of *Sagrina*, hitherto undescribed, but not uncommon at some of the "Challenger" stations, can only be distinguished with difficulty from the Clavuline group of *Textulariæ*, its most recognisable character, as in so many other instances, being a tubular neck. In conformation it accurately resembles *S. dimorpha*, P. and J.; the test is thin, but it is composed of fine sand-grains, of uniform size, firmly compacted. This species helps to connect the clear-shelled forms with the rough Cretaceous species described by d'Orbigny.

But the form now under consideration, *Sagrina divaricata*, presents in some respects a further deviation from the typical structure than the Clavuline variety alluded to, or, indeed, than any previously noticed. Its general features will be readily gathered from the description and figures. Specimens are rarely found entire owing to the tenuity of the connecting stoloniferous tubes, but in certain tropical shallow-water sands, fragments showing the neck, and sometimes one or two segments, are not unfrequent. In complete specimens the initial chambers are clustered into a little ball scarcely bigger than one of those subsequently formed.

The best examples that have been found occur in material from Humboldt Bay, Papua (37 fathoms), and off Tongatabu (18 fathoms).

GLOBIGERINIDA.

The *Globigerinida* form a large and diverse group, and almost every section of it acquires some fresh significance from the "Challenger" collections. Of the simple non-septate genus *Spirillina* several new forms are now to be described. The genus *Chilostomella*, first found in the recent condition two or three years ago by the Rev. A. M. Norman, is shown by the "Challenger" dredgings to have a wide distribution as a living type, and its near ally, *Allomorphina*, aforetime regarded as a rare Cretaceous and Early Tertiary fossil, is represented by recent specimens from two to three localities. *Pavonina*, concerning which little or nothing has been known beyond its general external appearance as depicted by d'Orbigny, is met with at two or three stations, and the difficulty which has been experienced by later Rhizopodists as to its zoological affinity is found to have arisen from the inaccuracy of the original figures. Of the Rotaline genera it is difficult to speak briefly, the number of species obtained is so large. Probably the result of their examination will be of value rather in the more accurate definition and better understanding of forms already known and named than in the number of new species to be described. There are, however, a few very distinct forms not previously recorded. Of these, two somewhat important *Pulvinulinæ*[1] have already been noticed, the published descriptions being founded upon "Challenger" specimens, and a striking little *Planorbulina* is described and figured in the present paper.

Of the genus *Globigerina* and its immediate allies a somewhat longer summary is needful—one that may serve as the basis of a subsequent detailed exposition of so important a group—and to this end certain new species, of which illustrative figures cannot at present be given for want of space, are introduced, as well as circumstances permit, by verbal descriptions.

Genus—SPIRILLINA, *Ehrenberg*.

The genera *Spirillina*, *Cornuspira*, and *Ammodiscus*, are isomorphous, and represent vitreous, porcellanous, and arenaceous types of structure respectively. The resemblance of the tests of some of these simple forms to the shells of pteropods and annelids, whilst often a source of difficulty where the imperforate *Cornuspira* and the sandy *Ammodiscus* are concerned, scarcely affects the diagnosis of *Spirillina*,

[1] "*Pulvinulina fusca*, and *P. Menardii*, var. *tumida*," 'Geol. Mag.,' 1877, Dec. 2, vol. iv. p. 535.

connecting link between the fully developed form and Williamson's *Spirillina margaritifera*,[1] hence the description furnished to my friend Mr. Siddall (*loc. cit.*) needs a little revision. In the specimens from our own shores the tubercular exostoses are frequently confined to the central portion of the test, which is otherwise a flat or slightly concave disc, bearing no indication of the spiral internal structure.

Well-marked individuals of this species are found in two of the dredgings off Kerguelen Islands, namely, in Royal Sound, 20 to 60 fathoms, and off Christmas Harbour, 120 fathoms.

Genus—CHILOSTOMELLA, *Reuss*.

CHILOSTOMELLA OVOIDEA, *Reuss*. Pl. VIII, figs. 11, 12.

Chilostomella ovoidea, Reuss, 1849. 'Denkschr. d. math.-nat. Cl. k. Akad. d. Wiss.,' vol. i, p. 380, pl. 48, fig. 12.
— *Czjzeki*, id. ibid., pl. 48, fig. 13.

The genus *Chilostomella* has until quite recently remained almost unknown to English Rhizopodists. It has never been found amongst the fossils of our microzoic deposits, and before its discovery by the Rev. A. M. Norman,[2] in sands dredged off Valentia (112 fathoms), and amongst material brought by the scientific staff of the "Valorous" from the far north, its range of distribution was supposed to be limited to certain Tertiary marls of Central Europe. It is nevertheless to be regarded as a locally or partially distributed rather than as a very rare recent type, for it occurs in considerable abundance in many areas far apart, and the wonder is that it remained so long unobserved.

The structural features of *Chilostomella* and its near ally *Allomorphina*, are so remarkable that Reuss very properly placed the two genera in a family by themselves, which he characterised as follows (*loc. cit.*):

"*Enallostegia cryptostegia*.—Testa libera, irregularis, inæquilatera, conflata e loculis perfecte amplectentibus, alternantibus, ad axes vel duos oppositos vel tres in triangulo positos. Contextura testæ vitrea, pellucida, nitens."

Seguenza's interesting genus *Ellipsoidina* is, I am convinced, very nearly related to the types included by Reuss in this family; and the descriptive characters above quoted would need but little modification to admit a form which differs chiefly from *Chilostomella* in the segments springing

[1] 'Rec. Foram. Gt. Br.,' p. 93, pl. 7, fig. 204.
[2] 'Proc. Roy. Soc.,' vol. xxv, p. 214.

uniformly from one end, instead of alternately from the two extremities.

The test of *Chilostomella* may be described in general terms as composed of a series of nearly symmetrical, ovate, or elliptical segments, each enclosing the whole of that previously formed, with the exception of a small portion of its end. The order of the segments is alternate, that is to say, they are put on first from one end, then from the other. The line of union is not directly transverse but dips towards one side, so that more of the penultimate chamber is exposed at one side than at the other. The aperture is crescentic, sometimes bordered by a thickened lip, and always situated on the margin of the final segment in the region nearest to the apex of the shell. In shape the test varies from an elongate, sub-cylindrical, to a short, rounded, oval, between which extremes every variety of contour may be met with; the ends are sometimes blunt and rounded, sometimes more or less tapering, so that, unless Professor Reuss's two species (*Ch. ovoidea* and *Ch. Czjzeki*) have some better distinguishing feature than mere size and external form, they may very safely be resolved into one. In deep water the specimens are often more delicate and transparent, and also more elongate than in shallow seas, but this is by no means an invariable rule. One or two individuals of this species have been found amongst the gatherings of surface Foraminifera, but there seems no reason to suppose that the type is essentially a pelagic one.

Chilostomella ovoidea has been met with at "Challenger" stations in the North Pacific, South Pacific, and North Atlantic. It also occurs in one or two of the "Porcupine" dredgings from more northerly areas in the Atlantic than any point of the "Challenger" voyage, and the Rev. A. M. Norman has obtained the species in some abundance on the coast of Norway. The recorded depths of the "Challenger" dredgings in which it has been found are nearly all between 300 and 600 fathoms, but one of them is as deep as 2300, and another as shallow as 95 fathoms.

Genus—ALLOMORPHINA, *Reuss.*

ALLOMORPHINA TRIGONA, *Reuss.* Pl. VIII, figs. 13, 14.

Allomorphina trigona, Reuss, 1849. 'Denkschr. d. math.-nat. Cl. k. Akad. d. Wiss.,' vol. i, p. 380, pl. 48, fig. 14.

— *cretacea*, Reuss, 1850. 'Haidinger's Abhandl.,' vol. iv, p. 42, pl. 5, fig. 6.

The genus *Allomorphina* differs from *Chilostomella* in

having three chambers to each circuit instead of the alternating two, and, as its growth takes place on one plane, the test assumes a sub-triangular and more or less depressed contour. There does not appear to be any morphological distinction between the two "species" above quoted, and mere difference of geological age is of little value from a zoological standpoint; nor can the fossil specimens be separated from the recent ones by any character of specific or even varietal significance. In the living condition *Allomorphina* is exceedingly rare, and the individual specimens are small and delicate. The genus is supposed to have made its appearance earlier than its ally *Chilostomella*, and it may in like manner be the first to die out.

In two dredgings only has *Allomorphina trigona* been found recent; one of these is from the *Hyalonema*-ground to the south of Japan, in 345 fathoms, the other, off Tahiti, in 620 fathoms.

Genus—PAVONINA, *d'Orbigny*.

PAVONINA FLABELLIFORMIS, *d'Orbigny*. Pl. VIII, figs. 29, 30.

Pavonina flabelliformis, d'Orbigny, 1826. 'Ann. Sci. Nat.,' vol. vii, p. 260, No. 1, pl. 10, figs. 10, 11:—Modèle, No. 56.

D'Orbigny obtained this rare and interesting Foraminifer from Madagascar prior to 1826, and from that time until a year or two ago, when I had the good fortune to meet with it in some sand dredged by my friend Dr. E. Perceval Wright, in shallow water in the Seychelle Islands,[1] it had not been found by any subsequent naturalist, and much doubt had been expressed as to its structure and affinity. Messrs. W. K. Parker and T. R. Jones suggested, in one of their papers on the Nomenclature of the Foraminifera,[2] that it might "possibly be a symmetrical Peneropolis, more probably a semi-discoidal modification of Orbitolites." But the specimens now brought to light show that its place is far from the porcellanous series, and that the morphological difficulty has arisen from a slight inaccuracy in d'Orbigny's figure and Model, which has probably arisen from defective microscopic powers. Careful examination of the specimens reveal the fact, not very clear at first sight, that the early chambers are not spiral or subspiral, as they appear to be,

[1] 'Ann. and Mag. Nat. Hist.,' 1877, ser. 4, vol. xix, p. 105.
[2] Ibid., 1863, ser. 3, vol. xii, p. 440.

and further that they do not reach the entire width of the test, but are laid on alternately. In other words, that the shell begins growth as a *Textularia*, and subsequently constructs a single series of large, flat, arched segments, which give it its fan-like contour. The shell-wall is thin and transparent, the perforations numerous and large, and the sutures limbate. The general aperture takes the form of a row of small orifices on the outer face of the terminal segment. The diameter of the largest specimen which has been found is $\frac{1}{39}$ inch (about 1·0 millim.).

Pavonina flabelliformis has been taken at three of the "Challenger" stations, namely, Nares Harbour, Admiralty Islands, 17 fathoms; off Culebra Island, West Indies, 390 fathoms; and off the reefs, Honolulu, 40 fathoms. These, with the habitats furnished by the researches of d'Orbigny and the material collected by Dr. Perceval Wright, represent our knowledge of the distribution of the species.

Genus—PLANORBULINA, *d'Orbigny*.

PLANORBULINA ECHINATA, *n. sp.* Pl. VIII, fig. 31, *a*, *b*, *c*.

Characters.—Test nearly spherical; composed of few segments, about four in the last convolution. Segments ventricose, unequally arched, embracing. Shell coarsely perforated and usually armed externally with short, blunt spines. Aperture large, round, sometimes partially closed by a shelly plate within the bordering lip. Diameter $\frac{1}{80}$ inch (0·32 millim.).

The affinity of this little organism to the *Rotalinæ* is easily determined, notwithstanding its anomalous shape; and the bordered neck which forms the aperture, together with the coarse perforation of the shell-wall, suggest its more intimate connection with the genus *Planorbulina*. It is a minute, inconspicuous species, and cannot well be confounded with any previously known.

Planorbulina echinata has its home amongst the coralline sands of shallow seas, and has been found at ten or twelve of the "Challenger" stations, chiefly amongst the islands of the Pacific. Except in one locality, Nares Harbour just south of the Equator, the number of specimens from any single habitat is very small.

Genus—GLOBIGERINA, *d'Orbigny*.

The extent and variety of the "Challenger" soundings and the large area over which the tow-net was employed during the expedition have furnished opportunity for a somewhat comprehensive examination of the shells of *Globigerina* and the allied genera. It would be impossible in a mere preliminary paper like the present one to treat the subject even briefly, in its numerous aspects, neither could it be done to any good purpose without the assistance of a large series of illustrative drawings. These will appear in due course, and with them some attempt at a complete history, but in the meantime there are one or two points that may be concisely touched upon, such as the range of morphological variation presented by the shells of the *Globigerinæ*, and the better definition of the quasi-specific forms, together with certain more general questions affecting the surface-fauna of the ocean so far as it consists of calcareous Rhizopoda.

Professors W. K. Parker and T. Rupert Jones, in their philosophical and valuable memoir on 'Foraminifera from the North Atlantic and Arctic Oceans,'[1] record the occurrence of only two species of *Globigerina* (proper), the typical *Gl. bulloides* and *Gl. inflata*; and in their supplementary tables recognise but two others, *Gl. helicina* and *Gl. hirsuta*. The limited number may be accounted for by the researches of these authors having been conducted chiefly amongst the northern and relatively stunted representatives of the group, and the characters assigned to the genus are, no doubt, more or less affected by the same circumstance. Their generic definition, which agrees in all essential points with Dr. Carpenter's more extended description,[2] runs as follows:

"The shell of *Globigerina* is composed of a series of hyaline and perforated chambers, of a spheroidal form, arranged in a spiral manner, and each opening by a large aperture around the umbilicus, in such a manner that the apertures of all the chambers are apparent on that aspect of the shell, and form a large 'umbilical vestibule'" (*loc. cit.*, p. 365). It will be seen as we proceed that these characters only apply to one section of the genus, and that possibly not the most important, and it may even be open to question whether *Globigerina bulloides*, the hitherto accepted type of the group, is really its best representative. I propose, therefore, to enumerate the "species" which I have found it

[1] 'Phil. Trans.,' 1865, vol. clv.
[2] 'Introduction,' p. 181.

necessary to recognise and to give briefly the distinguishing characters of each.

Globigerina bulloides, d'Orbigny ('Annales des Sci. Nat.,' 1826, vol. vii, p. 277, Modèles No. 17 and 76).—D'Orbigny described this species at four or five different times and never in quite identical terms, but his Model No. 76 may be accepted as a fair summary of the characters intended, and this presents the general features of the variety most abundant in the northern seas. The test is convex, the segments spherical and few in number, that is, about four in each convolution and seldom more than two convolutions, and the inferior surface is excavated at the umbilicus, forming a recess or vestibule into which the apertures of the individual segments are directed. In this simplest form we have a tangible and easily recognised starting-point. Though it does not represent the best development of the type it is the beginning of a chain, the successive links of which, some of greater some of less morphological significance, have none of them any pretension to rank as true species, but which collectively extend over an area of variation so large that the salient points must, of necessity, be distinguished by trivial names. The following notes indicate the directions in which these variations take place, the right precedence in nomenclature being as far as possible observed.

Globigerina dubia, Egger ('Neues Jahrb. für Min.,' 1857, p. 281, pl. 9, figs. 7—9)—represents the best development of the "*bulloides*" type. It has a fine, thick, regular shell with about three convolutions, each consisting of five or six segments. The segments are relatively small, the peripheral margin rounded and lobulate, and the umbilical vestibule deeply sunk.

Globigerina cretacea, d'Orbigny ('Mém. Soc. géol., Fr.,' vol iv, p. 34, pl. 3, figs. 12—14)—is, on the other hand, a starved form, of small dimensions, thin and flat-topped, the inferior surface concave. It also shows the umbilical vestibule, and differs from *Gl. bulloides* chiefly in its depressed contour, and the more compact fitting of the segments, especially the earlier ones.

Globigerina æquilateralis, nov.—This is a variety approaching *Hastigerina*, in general form. The test is planospiral and symmetrical, not Rotalian; it consists of but little more than a single convolution, and the whole of the segments are sometimes visible on both sides. The final segment is often smaller than the penultimate, as is sometimes also the case with *Gl. cretacea*.

Globigerina digitata, nov.—is a very singular modification of the type, and one that has not hitherto been described. The earlier segments are commonly regular and trochoid, but the later ones are much elongated and spreading. In some specimens, generally of small size, the final segment only is extended, like the index finger of the hand, but in others, two, three, or more chambers radiate in palmate fashion. The apertures of the chambers have thickened or lipped borders. It is a rare form, and usually of small size, $\frac{1}{50}$ inch (0·5 millim.), but in one dredging specimens have been met with measuring $\frac{1}{17}$ inch (1·5 millim.) in diameter.

Globigerina inflata, d'Orbigny ('For. Canar.,' p. 134. pl. 2, fig. 7—9)—is of plano-convex shape, the superior or spiral face being flat, the inferior convex. There is no umbilical vestibule, and the aperture of the last segment is the only orifice which is visible externally; this is large and gaping, and constitutes a distinctive feature. *Gl. inflata* is the isomorph of *Rotalia Soldanii* and *Pulvinulina crassa*, and it is even difficult sometimes to distinguish it from the latter species.

Globigerina Dutertrei, d'Orbigny ('Foram. Cuba,' p. 95, pl. 6, fig. 22—24).—I am disposed to recognise this as a convenient name for a small, thick, rounded variety, more compactly built than *Gl. bulloides*, and having no umbilical vestibule, but a single, comparatively small, arched orifice, with thickened lip. It has neither the flat superior surface nor the gaping aperture of *Gl. inflata*.

Globigerina rubra, d'Orbigny ('Foram. Cuba.,' p. 94, pl. 4, fig. 12—14)—exhibits, perhaps, the most important deviation of all from the type of structure with which we started. The test is more or less trochoid, often relatively very tall, and has about three segments in each convolution. The inferior surface has one arched aperture on the umbilical margin of the last segment, but many of the segments have either one or two large, more or less rounded orifices on their superior surface, close to the sutural depressions. Fresh specimens have a pink tinge, and the earlier chambers especially are often of very bright colour. It is to be regretted that d'Orbigny's name for this species should have been associated with so variable a characteristic as colour, the more so as in his description he makes prominent allusion to the numerous apertures. Several of the *Globigerinæ* show a tendency to pink colouration, though none to the same extent as *Gl. rubra*.

Globigerina conglobata, nov.—is a large subglobular modi-

fication of the "*rubra*" type, in which the early segments are small and compactly arranged, and the spire convex rather than trochoid; the later segments are large, particularly the three forming the final convolution, and disposed so as to give a convex base. The apertures on the superior surface are numerous, and the test is thick and coarsely perforated.

Globigerina sacculifera, Brady ('Geol. Mag.,' Decade ii, vol. iv, p. 535).—This is a distinct and conspicuous variety, briefly noticed in a short paper on the Foraminifera of a piece of white friable limestone from the New Britain Group (*loc. cit.*). It is characterised by its large outspread test, of of which the terminal chamber or chambers are pouch-shaped or pointed. The apertures on the superior surface are numerous; that of the final segment is sometimes directly over the inferior orifice, making a passage, as it were, right through the shell.

Globigerina helicina, d'Orbigny ('Ann. Sci. Nat.,' vol. vii, p. 279, No. 5;—Soldani, 'Testaceographia,' vol. i, pt. 2, pl. 130, figs. *pp*, *qq*, *rr*)—is an anomalous oblong form and one rarely met with. It is not easy to describe it intelligibly without the aid of figures. It most resembles an ordinary small Globigerine shell, with the addition of a little inflated chamber at two opposite points of its periphery. The superior surface is obscurely spiral and shows two, three, or more apertures. The inferior side has four visible segments; two large and oblong, laid side by side, and two small and inflated, one at each end of the test; the later have inferior apertures. It is possible that *Gl. helicina* may represent a monstrous condition rather than one of the more permanent varieties of the type. I have met with precisely analogous specimens in two other allied genera, and these have been treated as abnormal developments of the species to which they are related, namely, *Pullenia obliquelocula*ta and *Candeina nitida*. Justice has, perhaps, scarcely been done to the accuracy of Soldani's drawings in the present instance. Dr. Carpenter ('Introd.,' pl. 12, fig.) employs the name *Gl. helicina* for what appears to be only an immature specimen of a quite different variety (*Gl. sacculifera*). Of the three figures in the 'Testaceographia,' referred to by d'Orbigny, that marked *qq*, which gives both the superior and inferior aspects of the shell, is the most cha racteristic, and leaves nothing to be desired in point of defi nition.

There is little difficulty in distributing the *Globeriginæ* of

the "Challenger" collection amongst the salient types above enumerated, and the few exceptions that occur are chiefly in the case of specimens which are obviously monstrous. Nothing has been said of the spinous or hirsute surface-armature in the light of a zoological character, because it appears to possess no specific or even varietal value. Examples of almost every "species" embraced in the foregoing descriptions are met with from time to time, more or less covered with long silky spines, but such specimens are naturally much more common amongst those taken at the surface of the sea than in the contents of the dredge, and the spinous condition is more generally noticed in young and small than in fully-grown shells.

There are a few recorded forms, though very few, that cannot properly be asigned to any of the species in the foregoing summary. Of these, *Globigerina marginata* (Reuss)[1] is, perhaps, the most important, as it is one of the best defined Cretaceous forms. It belongs to the "*bulloides*" group, and to repeat the comparison with the genus *Pulvinulina*, it is the isomorph of *P. Menardii*, just as *Globigerina inflata* is the isomorph of *P. crassa*. I do not recollect ever having seen *Gl. marginata* in the recent condition, nor, indeed, otherwise than as a Cretaceous fossil.[2] Two other species, *Gl. elevata*, d'Orbigny, and *Gl. trochoides*, Reuss, have also been described from Cretaceous specimens, but I have been unable to identify them with any forms I am acquainted with. Both of them bear some resemblance to *Globigerina rubra* in their general features, the latter especially so, but the published drawings have no indication of orifices on the superior surface.

It will have been gathered from the foregoing *résumé* that the spiral *Globigerinæ* may be roughly divided into three groups on the basis of the position and character of the general apertures, and, to a less degree, on the contour of the test. These are—1st. The forms with an excavated cavity on the inferior surface ("umbilical vestibule"), into which the orifices of all the segments open—type, *Globigerina bulloides*. 2nd. Those with only one external orifice situated on the face of the terminal segment, at its point of junction with the previous convolution—type, *Gl. inflata*. 3rd. Those in

[1] *Rosalina marginata*, Reuss, 1845. 'Verstein, Böhm. Kreid,' pt. 1, p. 36, pl, 13, fig. 74. Figured better in a subsequent paper 'Denkschr. d. k. Akad. Wiss.,' vol. vii, pl. 26, fig. 1.

[2] It is possible that the *Rosalina Linnei* ('Foram. Cuba,' p. 106, pl. 5, 10—12, called *R. Linneiana* in the text), found by d'Orbigny on the of Cuba, may be the living representative of this species.

which the inferior aperture is single and relatively small, but is supplemented by conspicuous orifices on the superior or spiral surface of the test—type, *Gl. rubra*.

But, in addition to the spiral *Globigerinæ*, or rather those that appear so externally, there are certain spherical forms constituting the reputed genus *Orbulina*. Without entering into minutiæ, *Orbulina* may be defined as a minute, thin-walled, Globigerine shell enveloped in a large globular final chamber. Examples are not wanting, amongst other genera, of varieties leading up to similar conditions, but in none is the phenomenon so completely developed. In my previous paper I have indicated the fact, suggesting, by its uniformity, a general law, that when a Foraminifer forms an abnormally large segment, growth is arrested and no more chambers are produced. Amongst spiral Foraminifera *Cymbalopora bulloides* affords the most familiar example of a species with a balloon-shaped final segment, but the same peculiarity is developed in a less degree in certain modifications of *Discorbina* and *Pulvinulina*. All these forms have another character in common with *Orbulina*, namely, a double series of perforations; that is to say, the wall of the inflated chamber has two sorts of orifices, differing in size, the one set numerous and uniformly very minute, the other uniformly large and fewer in number.

The question arises whether the characters exhibited by these Orbuline forms are to be regarded as of mere varietal significance or as sufficient to warrant subgeneric or generic distinction. The reply seems to be, that the close affinity to *Globigerina* is best expressed and zoological convenience is best served by accepting *Orbulina* as a subgeneric type of that genus.

Globigerina (*Orbulina*) *universa*, d'Orbigny ('Foram., Cuba,' p. 35, pl. 1, fig. 1)—is figured by d'Orbigny, Williamson and others as a small spherical shell of yellowish hue, with a neat, round, general aperture in addition to the perforations that have been already alluded to; but Pourtales, Williamson, and Carpenter have all dwelt on the fact that this large orifice only appears in a minority of the specimens found. I am inclined to go a good deal further and, though not prepared to say that it does not sometimes exist, I believe it to be very rarely indeed that a fresh shell possesses what has any claim to be considered a general aperture. After looking over thousands of specimens I have not been able to find one from which a drawing like those of the text-books could be made. In dredged specimens large orifices

are not uncommon, but they occur, as often as not, two or three to a shell, and they either have abrupt angular edges, indicative of accidental fracture, or they are found at spots where the shell has been previously worn very thin. It must be remembered that the nature of the perforations which already exist in the shell-wall is one peculiarly favorable to the formation of larger orifices by abrasion or pressure. The matter, perhaps, is not one of very great consequence, seeing that it is admitted on all hands that a general aperture is not an essential or even a usual characteristic of *Orbulina*. In *Cymbalopora* under similar circumstances the general aperture is wanting, and a series of large perforations, in addition to the normal minute ones, takes its place, and there are other types of Foraminifera that have a number of conspicuous pores on the face of the terminal segment when it is of abnormally large size. It appears to me clear, therefore, that of the two sets of perforations in *Orbulina*, the larger ones stand in lieu of the aperture or apertures of the normal Globigerine shell.

Gl. (*Orbulina*) *neojurensis*, Karrer ('Sitzungsb. d. k. Akad. Wiss.,' vol. lv, p. 368, pl. 3, fig. 10).—The surface of the test in many species of helicoid *Globigerinæ* often bears a sort of honeycombed or reticulate ornamentation, best observed in specimens collected at the surface of the sea. This peculiarity is seldom met with in the Orbuline varieties, but Dr. Karrer has described and figured such a specimen amongst other fossil microzoa from the "White Jura" of St. Veit, near Vienna, under the name above quoted. Dr. Wallich has a drawing of a similar shell in his memoir on the "North Atlantic Sea-bed," pl. 6, fig. 9, and examples of the same form have been met with both by the Rev. A. M. Norman and myself in recent *Globigerina*-ooze; but, both in the recent and fossil condition, the variety is exceedingly rare.

Under the name *Globigerina bilobata* ('For. Foss. Vien.,' 164, pl. 9, fig. 11—14) d'Orbigny has figured what ars to be only a double *Orbulina* with slightly reticulated ace. Monstrosities of this kind are by no means uncom- wherever *Globigerinæ* abound, and sometimes, though frequently, specimens with two supplementary chambers, on each side of the parent-cell, may be met with. On grounds it does not seem worth binomial distinction.

Genus—HASTIGERINA, *Wyville Thomson.*

HASTIGERINA PELAGICA, (*d'Orbigny*).

Nonionina pelagica, d'Orbigny, 1839. 'Foram. Amér. Mérid.,' p. 27, pl. 3, figs. 13, 14

Globigerina pelagica, Parker and Jones, 1865. 'Phil. Trans.,' vol. clv, p. 336.

Hastigerina Murrayana, Wy. Thom., 1876. 'Proc. Roy. Soc.,' vol. xxiv, p. 534, pls. 22, 23.

An organism very closely allied to *Globigerina*, with which it corresponds also in its pelagic habit. It is not easy to find zoological characters to separate the two genera, but the nautiloid symmetry of the test of *Hastigerina*, its extreme tenuity, the embracing contour of the successive convolutions (the constituent chambers of which spring from the umbilicus on either side), and the large opening on the face of the ultimate segment that serves as the aperture, are perhaps its distinctive peculiarities. The empty shells are seldom found amongst dredged sand or ooze, and when they do occur they are invariably much broken, owing to the delicacy of the calcareous walls. When living the test is armed with long spines, but the bases of these alone are left in the dead shells found at the bottom.

Under the name *Nonionina pelagica*, d'Orbigny describes and figures what is manifestly the present species (*loc. cit.*), and appends the following remark:—"Cette espèce est une rare exception parmi les Foraminifères essentiellement cotiers, puisque nous l'avons prise en pleine mer, à une grande distance des côtes du Pérou, dans l'océan Pacifique, par 20° de latitude sud et 89° de longitude ouest de Paris, où elle nous a paru très rare." His figure represents a shell somewhat flatter than most of the "Challenger" specimens, with the sutures and umbilicus rather more depressed, and if these characters should be found sufficient to distinguish the two, Sir Wyville Thomson's specific or varietal name might be retained for the more spheroidal form.

Genus—CANDEINA, *d'Orbigny.*

CANDEINA NITIDA, *d'Orbigny.*

Amongst the Foraminifera from various habitats figured by d'Orbigny in the final plate of his "Vienna Basin" monograph,[1] are several that have been a source of difficulty to subsequent Rhizopodists, perhaps none more so than *Can-*

[1] 'For. Foss. Vien.' p. 593, pl. 21, fig. 28.

deina nitida. Except its recent mention by name amongst the species found by the Rev. A. M. Norman in the dredged material obtained on the "Valorous" cruise, I cannot find that it has been the subject of actual observation with any author since d'Orbigny's time, and hence conjectures as to its position and affinity have fallen somewhat wide of the mark. Max Schultze, in his scheme of classification,[1] places *Candeina* in the Subfamily *Uvellida*, between *Guttulina* and *Globulina*, two sections of the genus *Polymorphina*; and Von Reuss,[2] after expressing uncertainty as to its right zoological position, suggests that it possibly represents a new and distinct family, or if not, that perhaps it might be classed with the *Polymorphinæ*.

The genus *Candeina* does represent a distinct type of Foraminifera, but not a distinct family. Its affinity is to *Globigerina*, and, with specimens to refer to, its characters are easily comprehended. The test is spiral and trochoid, the segments globose, and usually three to each whorl. The earlier chambers are minute, the later ones relatively very large; the test is exceedingly thin and smooth and has a slightly yellowish tinge; the perforations are so fine that under a moderate magnifying power it appears imperforate. Instead of a single general aperture it is provided with a series of little rounded orifices, following the septal lines, most noticeable on the sutures of the later chambers, and seen on both the superior and the inferior surface of the test. In this respect it resembles the *Globigerinæ* of the "*rubra*" group, but the orifices are smaller and more numerous and they are regularly disposed.

I have found *Candeina nitida* amongst other pelagic Foraminifera from one surface gathering (Philippine Islands). Its occurrence in the "Challenger" bottom-dredgings is pretty much confined to the South Atlantic and South Pacific. D'Orbigny states (*loc. cit.*), "Nous n'en avons qu'une seule espèce des Antilles. Nous dédions ce genre à M. Ferdinand de Candé."

Notes on Pelagic Foraminifera.

employment of the towing-net during the cruise of hallenger" to an extent never before attempted, careful preservation of the animal and vegetable as collected by its means, have furnished the ground- not only for a better appreciation of the nature and

[1] 'Ueber den Organ. Polythal.,' p. 52.
[2] 'Sitzungsb. d. k. Akad. d. Wiss.,' vol. xliv, p. 384.

conditions of life at the surface of the ocean, but also for a more accurate comparison of its fauna with that of the sea-bottom than has heretofore been possible.

The earliest allusion to Foraminifera taken at the surface of the sea is probably d'Orbigny's note on "*Nonionina*" *pelagica* which has been already quoted; this was in the year 1839. There is no difficulty in identifying the drawings of the specimens then found with Sir Wyville Thomson's *Hastigerina Murrayana*, or its congeners.

In 1857, Mr. J. D. Macdonald[1] figured a small spinous *Globigerina*, which he describes as "the species most usually taken at the surface of the ocean." In the spring of the same year Dr. Wallich and Captain and Mrs. Toynbee appear also to have collected pelagic *Globigerinæ*, but no considerable addition was made to our knowledge of the subject until ten years later, when Major S. R. I. Owen contributed to the 'Journal of the Linnean Society'[2] a paper "On the surface-fauna of Mid-Ocean," which contained our first detailed account of pelagic Rhizopoda, and the first intimation of the fact that the genus *Pulvinulina* was almost as important a constituent of the surface-fauna as *Globigerina* itself. Major Owen's gatherings contained the following forms—I give them under the names employed in his paper—

Globigerina bulloides, d'Orb.
— *hirsuta*, d'Orb.
— *inflata*, d'Orb.
Gl. (*Orbulina*) *universa*, d'Orb.
— — *continens*, Owen.
Gl. (*Orbulina*) *acerosa*, Owen.
Pulvinulina Menardii, d'Orb.
— *canarinensis*, d'Orb.
— *Micheliniana*, d'Orb.
— *crassa*, d'Orb.

Three of these have, as I think, no claim to rank as species or even as named varieties—but this is a question that need not be debated here.

Since Major Owen's memoir the only recorded observations bearing on the subject are to be found in the brief notes sent home from time to time by the "Challenger" staff, and in the summary of the zoological work accomplished on board the vessel, furnished by Mr. Murray for the 'Proceedings of the Royal Society' in 1876.[3] These refer chiefly to points connected with the life-history of *Globigerina* and *Hastigerina*.

Facilities have been afforded me for the examination, not merely of the extensive series of mountings made by Mr. Murray on the spot from the contents of the tow-net, but also of portions of the various bottles of surface organisms

[1] 'Ann. and Mag. Nat. Hist.,' ser. 2, vol. xx, p. 266, pl. 7.
[2] 'Journ. Linn. Soc. Lond.,' 1867, vol. ix, "Zoology," pp. 148—157, pl. 5.
[3] 'Proc. Roy. Soc.,' vol. xxiv, p. 471—544.

which were preserved in bulk, and I have been enabled thereby to increase considerably the category of known pelagic species. The following list is as nearly complete as I am at present able to supply, but it is not improbable that there may be one or two varieties of *Globigerina* still to add. The *Globigerina hirsuta*, *Gl.* (*Orbulina*) *acerosa*, and *Gl.* (*Orb.*) *continens*, of Major Owen's paper, are all abundant in the "Challenger" gatherings, but their characters do not appear to be sufficiently distinctive nor sufficiently uniform to warrant separation from their congeners, and they have, therefore, been omitted from the list, or rather, are included in the species to which I believe them to belong.

Globigerina bulloides, d'Orb.
— *inflata*, d'Orb.
— *rubra*, d'Orb.
— *sacculifera*, Brady.
— *conglobata*, nov.
— *æquilateralis*, nov.
Gl. (*Orbulina*) *universa*, d'Orb.
Hastigerina pelagica (d'Orb).
— — var. *Murrayana*, Wy. T.
Pullenia obliqueloculata, P. and J.
Sphæroidina dehiscens, P. and J.
Candeina nitida, d'Orb.
Pulvinulina Menardii (d'Orb).
— — var. *tumida*.
— *canariensis* (d'Orb).
— *crassa* (d'Orb).
— *Micheliniana* (d'Orb).
Cymbalopora bulloides, d'Orb.
Chilostomella ovoidea, Reuss.

Some few of these, notably *Candeina nitida* and *Chilostomella ovoidea*, are of extreme rarity in the surface gatherings, whilst *Hastigerina pelagica* and *Cymbalopora bulloides*, though tolerably abundant at times, are very local in their distribution.

So much has been written on the relation of the surface Rhizopod-fauna to the organic remains found at the sea-bottom, and the conclusions arrived at by different observers are so diverse, that a brief statement of the facts brought into prominence by these investigations, may not be without its use. On a question concerning which so little in the nature of positive evidence can be adduced, it is necessary to speak with great caution, and it is possible that even now we are not in a position to arrive at more than provisional inferences. My own observations have been directed, firstly, to the comparison of the general aspect of the fauna of the surface with that of the bottom; and secondly, to the comparison of individuals of the several species found under the two conditions, in respect to their shell-structure and similar particulars.

The list that has just been given includes all the species known to enjoy a pelagic existence, and of the forms enumerated two or three of the rarest need not be taken into account. *Hastigerina* may be dismissed in a word; it is

probably an exclusively pelagic type, and I have never met with a dredged specimen the shell of which was more than approximately complete. A comparison of *Cymbalopora bulloides* with two or three species of the same genus not having the large globular chamber would lead to the belief that it also may be of essentially pelagic habit.

But it is with the genera *Globigerina* and its immediate allies, and *Pulvinulina*, that we are chiefly concerned in the present inquiry. Of nine recent species, or well-marked varieties of *Globigerina* (proper), at least two-thirds occur in the surface gatherings; indeed, though there are three or four forms that have not been satisfactorily traced, the only ones conspicuous by their absence are *Gl. dubia*, which represents the most finely developed modification of the "*bulloides*" type, and *Gl. digitata*, the most divergent of all from the normal form in its structural features. The Orbuline *Globigerinæ* are represented by *O. universa* in thin-shelled condition, and the absence of the very rare *O. neojurensis* need not excite surprise.

Amongst the *Sphæroidinæ*, the thick-shelled *Sph. dehiscens*, with its coarsely tubulated walls, is not uncommon, whilst the thin-shelled *Sph. bulloides* has never been met with at the surface. One species of *Pullenia* (*P. obliqueloculata*) is found sparingly at the surface, whilst the two smaller forms, *P. sphæroides* and *P. quinqueloba*, are only known from dredged specimens. Lastly, *Pulvinulina* supplies at least five forms to the surface fauna, all of them pertaining to one section of the genus: of these, two are rare, *P. crassa* and *P. Menardii*, var. *tumida*, and of them the number of specimens found is insufficient for purposes of comparison or argument; the rest are very common. Other *Pulvinulinæ*, found in abundance in dredgings from great depths, have never been obtained by the towing-net.

If the *Globigerinæ* obtained from the surface of the ocean are compared with specimens of the same species collected by the dredge, certain differences are at once apparent, the most conspicuous of which is the frequency of hirsute or spinous shells in the former, and their comparative absence from the latter source. This is so readily accounted for that it need not be dwelt upon. It has already been stated that nearly all the morphological varieties of *Globigerina* may be found at times covered with these long silky spines; and on the other hand, though the spinous condition is very frequent in pelagic shells, it is by no means invariable.

Another point of some importance is the relatively smaller size of the surface specimens. This has been made the

subject of careful investigation, the largest pelagic specimens of each species having been measured side by side with good average examples from bottom-dredgings. The result has been to demonstrate that, with the possible exception of the *Orbulinæ*, concerning which I shall have to speak presently, the largest of those collected at the surface are smaller than average adult bottom specimens. In all the species this difference in size is apparent, though in some more than others, but if drawings are made to the same scale the rule becomes strikingly manifest. It would be easy to give measurements in support of this point, but it seems better to wait until the matter can be fully discussed with the aid of plates.

The thickness of the tests of some pelagic specimens has been the ground of remark, and viewed by themselves the largest examples of certain species are very stoutly built, but as a matter of actual measurement they will not bear comparison with those found at the bottom. Thus, the stoutest specimen of *Sphæroidina dehiscens* which I have been able to find amongst the surface gatherings has a test of about $\frac{1}{500}$ of an inch (0·05 millim.) in thickness, and the heaviest-shelled *Globigerina conglobata* so collected is not more than $\frac{1}{800}$ of an inch (0·032 millim.), whilst bottom specimens of either species, having shells $\frac{1}{300}$ of an inch (0·085 millim.) in thickness, are not unusual.

The case of *Orbulina* is somewhat different. The shells of surface specimens are nearly as large as those of average size from the bottom, but, whether spinous or not, they are invariably very thin and delicate. Bottom specimens are not only thicker, but vary very much amongst themselves in shell texture and other particulars. The most noteworthy structural condition found amongst the bottom specimens is one in which the shell consists of a number of distinct superimposed layers—sometimes four or five separate shelly envelopes—one enclosed within the other, yet without any absolute adhesion of their walls. In such cases the innermost layer is usually very thin and perforated with large foramina, the outer ones coarser and thicker. Nothing resembling the thick-shelled *Orbulinæ*, still less those with multiple tests, has, so far as I know, been noticed amongst the surface organisms.

There is another fact connected with the subject which has a certain amount of weight, namely, that though the towing-net has been largely used in the British seas and in areas at which *Globigerinæ* are found to a greater or less extent at the bottom, no single specimen has been met with

amongst the Entomostraca and other pelagic microzoa that have been captured.

At best the evidence afforded by comparative observations is collateral rather than direct, and the only positive testimony that could be adduced would be such as the sea-bottom itself could alone furnish, and of a sort not easily procured. Material brought up in large quantities by heavy dredges and trawls is manifestly valueless for the purpose. Under any circumstances living microzoa would not be found except in the superficial film of the ocean-floor, and even there they would be largely mixed with dead and empty shells; it would therefore be simple waste of time to decalcify *Globigerina*-ooze obtained in the ordinary way with the idea of finding the protoplasmic bodies of the constituent shells. Indeed, it would be almost as reasonable to expect to find sarcode animals in a fossil deposit as in material possibly representing a layer several inches in thickness of the sea-bottom. The old methods of taking soundings, either with the lead and tallow or with some of the smaller appliances that succeeded it, though of comparatively little utility for the general purposes of zoological investigation, were perhaps better adapted for securing a knowledge of the superficial layer; and it is even possible that some of the discrepancies in the results obtained by different observers may be explained through the different methods by which their material has been collected.

But, in addition to dredge and trawl, another appliance was used from time to time by the "Challenger" naturalists in bottom-collecting. This was a towing-net attached to the trawl, intended to receive the organisms thrown up by the rough disturbance of the superficial layer of the bottom-mud. It was without any great expectation of positive results that I determined to experiment on some of the material obtained by its means, inasmuch as shells more or less filled with sarcode might not be those longest held in suspension, though the difference in specific gravity between sarcode and sea-water cannot be very great. But the result has been satisfactory as far as it goes, and in one case the sarcode bodies of six or eight per cent. of the shells operated upon were left after treatment with acid. Amongst these were easily recognised specimens of *Globigerina*, *Pulvinulina Menardii* and *Sphæroidina dehiscens*. The sarcode was yellowish-brown and granular, precisely resembling that of in-shore Rhizopoda that have been kept some time in alcohol before being decalcified. The soft, jelly-like lobes of *Sphæroidina* retained the form of the pseudopodial tubulation

of the shell as minute, cylindrical projections from the surface.[1] Without departing from an attitude of caution in accepting evidence upon a subject so beset with difficulty, I will endeavour in a few words to summarise the facts bearing upon it, chiefly on those concerning the two genera *Globigerina* and *Pulvinulina*.

1. We have positive evidence that Foraminifera do live at the bottom of the deep sea, from the common occurrence at great depths of certain forms with composite or arenaceous tests; and we have negative evidence in the same direction in the entire absence from the surface fauna of many hyaline genera, which are abundant in bottom dredgings.

2. Both in *Pulvinulina* and *Globigerina* (but notably in *Pulvinulina*) species closely allied to the surface forms are common in the bottom ooze, though they never occur at the surface; amongst others, *Globigerina dubia* and *Gl. digitata*, *Pulvinulina elegans*, *P. Karsteni*, *P. pauperata*, and *P. favus*. Hence there is no *à priori* improbability that the other members of the same genera are capable of supporting life at the bottom.

3. A comparison of specimens of the same species, taken at the surface and at the bottom, demonstrates at least that the average size of the former is less than of the latter, and that the thickness of the shell-wall of the largest surface specimens bears no comparison with that of adult bottom specimens.

4. Nothing comparable to the thick-shelled *Orbulinæ*, still less to those with tests composed of several layers, is to be met with in the surface fauna.

5. No surface *Globigerinæ* have hitherto been obtained by means of the towing net from points on our own shores at which they are found at the bottom.

6. A fact adduced by Dr. Wallich, of some weight, as I think, namely, that *Globigerina* shells are found in the

[1] I find a note of Dr. Wallich's, in a lecture delivered before the Royal Institution, in 1861, the substance of which appeared, I believe, in one of his earlier papers, which is quite in accordance with these results. Speaking of a particularly pure *Globigerina* deposit he says:—"The specimens from the immediate surface stratum of the sea-bed alone retained their normal appearances, both as regards the perfect state of the sarcodic contents of the shells and the presence of the pseudopodia. The latter organs were never seen by me in an extended position, but in the specimens alluded to, and in those only, the pseudopodia occurred as minute bosses, resembling in shape the rounded rivet heads on boilers, closely adpressed to the external surface of the shell."

digestive cavities of *Ophiocomæ* living at the bottom at great depths.

7. The testimony of many experienced observers (Ehrenberg, Parker and Jones, Wallich, and others) that the *Globigerinæ* in the small soundings which they had for examination contained the sarcode bodies, the colour and nature of which each has described, with which statement my own results from the material taken in the "tow-net attached to trawl" generally agree.

It may be that some of these arguments bear an explanation other than that which appears the most natural one. The only facts that I know of, *per contra*, are—

1. The dredged or trawled material consists of nothing but dead or empty shells.
2. Dredged specimens from great depths have never been observed to extend their pseudopodia.

The first of these propositions, as I have already shown, scarcely, in reality, affects the question. In respect to the second, it is to be observed that the same holds good of the arenaceous Rhizopoda, which we know live at the bottom. Neither will any one who has had much experience in handling shallow-water Foraminifera, and knows the difficulty there often is in inducing a common *Rotalia* to extend its pseudopodia after being taken out of an aquarium and put into a watch glass, wonder much at the want of this particular evidence of life in specimens whose whole environment has been thus suddenly changed — released from enormous pressure and brought from darkness into strong light.

In addition to its employment at the surface of the sea, the tow-net was used by the "Challenger" naturalists suspended at different depths in the water, and pelagic Foraminifera were collected with other forms of animal life hundreds of fathoms below the surface. I confess, therefore, that I can see no anomaly in the supposition that organisms so simply constituted as this group of Protozoa may be equally at home at the surface and at the bottom of the ocean.

The Morphology *of the* Vertebrate Olfactory Organ.

By A. Milnes Marshall, M.A., D.Sc., Fellow of St. John's College, Cambridge. (With Plates XIII and XIV.)[1]

Of the two parts into which the present paper is divided, the first deals with the development of the olfactory nerve in certain selected types of vertebrates; the second with the development of the olfactory organ in the same types.

Since the value and interest of anatomical and embryological facts consist largely in their application to the solution of morphological problems, I have not hesitated to draw inferences freely from such facts as I have been able to bring to light, or to point out the conclusions to which these facts seem to me to lead. However, in order to separate facts from theories as sharply as possible, each part of the paper has been further subdivided, those portions which are concerned with matters of direct observation being considered before those which are of a more theoretical or speculative nature.

I. *The Development of the Olfactory Nerve.*

a. In the dogfish.—For the opportunity of investigating the development of Elasmobranchs I am indebted to Mr. Balfour, who, on the completion of his monograph on Elasmobranch fishes, very kindly placed at my disposal the whole of his stock of uncut embryos. In addition to this I have had the great advantage of free access to the very complete series of preparations made by Mr. Balfour in the course of his investigations, and have availed myself of his permission to figure four specimens, illustrating stages of which I had not prepared satisfactory sections myself.

The greater number of the embryos thus placed in my hands were those of the *Scyllium canicula*, some few of *Pristiurus;* but inasmuch as the two genera have yielded identical results so far as the subject in hand is concerned, I have made no attempt to distinguish between them either in my descriptions or figures. Some few of the specimens were hardened in picric acid, and afterwards stained with hæmatoxylin; but all my best sections were from embryos hardened and stained in a ¼ per cent. solution of chromic acid, to which a few drops of a weak solution of osmic acid had been added.

[1] An abstract of this paper was read before the Royal Society on February 13th, 'Proc. Roy. Soc.,' No. 193, 1879.

With regard to the earliest stages in the development of the olfactory nerve, I have, unfortunately, been unable to make any satisfactory observations, for all the specimens younger than Balfour's stage K were in bad condition. The chief points I wished, if possible, to determine were—firstly, whether the neural ridge extends to the anterior end of the fore brain in Elasmobranchs, as I have already shown it to do in the chick ;[1] secondly, whether the olfactory nerve is developed from this ridge; and, lastly, the exact date of appearance of the olfactory nerve. On all these points I have, owing to the unsatisfactory condition of my specimens, failed to obtain reliable evidence.

Plate XIV, fig. 19, represents a section through the head of a dogfish embryo at stage M of Balfour's nomenclature; the section is made in a plane transverse to the longitudinal axis of the head, and passes through the fore brain (*f. b.*), the olfactory sacs (*olf.*), and the olfactory nerves (I).

This figure, which is taken from one of an excellent series of preparations in perfect histological preservation, illustrates several features of considerable interest—(1.) In the first place it will be noticed that the fore brain presents no trace whatever of a division into cerebral hemispheres; in other words, that *the olfactory nerves come into existence before the cerebral hemispheres*, and are therefore connected at first with the forebrain, and not with the hemispheres. As confirmation of this point, I may repeat that fig. 19 is taken from an embryo at stage M, while Balfour has already shown, and my own observations are in complete accordance with his on this point, that until stage O there is no trace whatever of a division of the forebrain into cerebral hemispheres.[2]

(2.) *There is no trace of an olfactory lobe or vesicle.* This is a point of considerable importance, and one on which I desire to lay stress. The figure shows that at stage M the olfactory nerves are solid, and present no trace of a central lobe or vesicle, either at their roots or at any part of their length.

(3.) The olfactory nerve at stage M agrees closely in its general relations and in its histological characters with the other cranial nerves, either at the same or at slightly younger stages. Like these, it arises from the upper part of the

[1] 'Quarterly Journal of Microscopical Science,' January, 1878, pp. 13—16.

[2] 'Elasmobranch Fishes,' p. 178.

sides of the brain, and takes a course downwards and outwards, at right angles to the longitudinal axis of the head. Histologically it consists of roundish or oval nucleated cells, with, as yet, very few nerve fibres, agreeing completely with corresponding stages of development of the other cranial nerves.

Fig. 20 is taken from a section through the same region as fig. 19, but from a dogfish embryo at the commencement of stage o. The magnifying power employed is the same in the two drawings, so that an exact comparison can be made between them. There is still no indication of a division into cerebral hemispheres; the forebrain, as in fig. 19, is still undivided. Though the embryo has grown considerably the olfactory nerve (1), though somewhat thicker, is no longer in fig. 20 than in fig. 19, a fact of some interest; its point of attachment to the brain has, however, shifted down somewhat towards the ventral side. The most important fact shown by fig. 20 is, however, the existence of the earliest rudiment of an olfactory lobe (*ol. v.*). This, as may be seen from the figure, is exceedingly small, and might indeed be easily overlooked; it is a small shallow pit, formed almost entirely at the expense of the inner wall of the forebrain, and situated opposite the root of origin of the olfactory nerve.

In fig. 21, taken from one of Mr. Balfour's specimens, the same parts are shown at a stage intermediate between stages o and P. The olfactory vesicle (*ol. v.*) is seen to have grown very rapidly, and is now a conspicuous object. The olfactory nerve (1), on the other hand, has remained almost stationary as far as size is concerned; it has, however, undergone considerable histological change; the cells composing its proximal part or root of origin are more elongated and fusiform than before, while beyond this part the nerve presents a ganglionic expansion consisting mainly of roundish cells, similar to those which previously constituted the whole nerve, and which gives off, distally, bundles of nerve fibres distributed to the Schneiderian folds of the olfactory mucous membrane.

The condition of the olfactory nerve and lobe at stage Q is shown in fig. 22, also taken from one of the specimens lent me by Mr. Balfour, who has described this stage as follows:—"The lateral ventricles are now separated by a median partition, and a slight external constriction marks the lobes of the two hemispheres; these, however, are still united by nervous structures for the greater part of their extent. The olfactory lobes are formed of a distinct bulb and stalk,

and contain, as before, prolongations of the lateral ventricles."[1]

It will be noticed that, while in fig. 21 the olfactory lobe projects out at right angles to the brain, and the olfactory nerve arises from its extreme tip, in fig. 22 the olfactory lobe is bent downwards, so as to lie against the side of the cerebral hemisphere, and the olfactory nerve no longer arises from its apex, but slightly from its dorsal surface. From the condition here represented to that of the adult the changes are unimportant.

The earlier stages of the olfactory nerve I have not been able to work out satisfactorily, for reasons already mentioned. In fig. 15 the nerve is represented in longitudinal and vertical section at stage M. It is easily recognisable at stage L, and I have also succeeded in satisfying myself of its existence as far back as stage K.

Fig. 14 represents a transverse section through the anterior part of the head of an embryo at the commencement of stage K; the section passes through the forebrain, and through both olfactory pits; on the right side a small mass of cells (I) in contact with the bottom of the pit is stained rather more deeply than the surrounding mesoblast cells. From comparison with the condition of what is undoubtedly the olfactory nerve at slightly later stages, I consider it very probable that these cells form part of the olfactory nerve, but cannot, of course, speak with any certainty on this point. Apart from the insufficient material at my disposal, the inherent difficulties of the investigation are very great, for at these early stages the olfactory nerve consists entirely of cells, which differ but little from the surrounding mesoblast cells; the nerve is also exceedingly short, owing to the close proximity of the olfactory pit to the brain, while a new difficulty is introduced by cranial flexure, which is increasing rapidly about this time, and so causes a constant shifting in the relations of the surrounding parts to one another.

My investigations, then, lead me to give the following account of the development of the olfactory nerve in Elasmobranchs. The nerve arises at some period earlier than stage K; it is at first connected with the upper part of the side of the forebrain; between stages L and O its root shifts downwards to a certain extent towards the ventral surface; the nerve itself is, from the earliest period at which it can be recognised, solid; the earliest trace of an olfactory lobe appears at the commencement of stage O as a shallow depression of the inner wall of the forebrain opposite the root of

[1] Op. cit., p. 179.

the olfactory nerve; this olfactory lobe grows very rapidly, and soon attains a large size, while the olfactory nerve remains almost stationary; the nerve is at first connected with the apex of the olfactory lobe, but subsequently mounts somewhat on to its dorsal surface; finally, the olfactory nerve, throughout its development, agrees closely in histological characters and in the changes which it undergoes with the other cranial nerves.

Balfour has given a somewhat different account of the development of the olfactory nerve. After noticing that the olfactory lobes first arise during the stage o, he says:—"From the peripheral end of each olfactory lobe a nerve, similar in its histological constitution to any other cranial nerve, makes its appearance; this divides into a number of branches, one of which passes into the connective tissue between the two layers of epithelium in each Schneiderian fold. On the root of this nerve there is a large development of ganglionic cells. I have not definitely observed its origin, but have no reason to doubt that it is a direct outgrowth from the olfactory lobe, exactly similar *in its mode of development* to any other nerve of the body."[1] A little further on he remarks: "Even the few preparations of which I have given figures appear to me to prove that . . . from the (olfactory) bulb a nerve grows out which has a centrifugal growth like other nerves of the body, and places the central olfactory lobe in communication with the peripheral olfactory sack."[2]

The differences between this account and my own are sufficiently obvious. According to Balfour, the olfactory lobe exists before the olfactory nerve, and the nerve is a "direct outgrowth from the olfactory lobe." A minor point of difference is that, according to Balfour, the connection between the olfactory nerve and the olfactory pit is not acquired till towards the end of stage o. I believe, however, that these differences are due to Balfour having overlooked the existence of the olfactory nerve during its early stages. The first stage at which he has described the olfactory nerve is that which I have represented in fig. 21,[3] while the specimens I have figured (figs. 19 and 20) appear to me to prove indisputably the existence of the olfactory nerve at a much earlier period, and the connection between the olfactory nerve

[1] Op. cit., p. 178.
[2] Op. cit., p. 183.
[3] The section from which this figure is drawn is one of the same series, if not the identical specimen, as that described by Balfour, and figured by him in Pl. XV, fig. 2.

and olfactory pit appears to be acquired at least as early as stage K.

b. In the chick.—I propose to consider the chick next, partly because, having devoted more time to the embryology of the chick than of other vertebrates, I have a better and more complete series of preparations to refer to, and partly because I wish to direct particular attention to the very close correspondence that exists between the chick and the dog-fish in the mode of development of the olfactory nerve.

Concerning the early stages of the olfactory nerve in the chick I have little or nothing to add to the account I have already given in this Journal.[1] The result of a careful re-examination of my former preparations, and the investigation of a considerable number of new specimens prepared since my former paper was published, has been to confirm my previous description on all points. Though I have again failed to trace satisfactorily the changes that occur between the thirtieth and fiftieth hours my further work has shown no reason for altering the view I have previously expressed, that the olfactory nerve is developed, like all the other cranial nerves (except the optic, the sixth, and (?) the fourth nerve), from the *neural crest*[2]. However, whether this be so or not is of comparatively little importance to the subject with which we are now concerned.

Plate XIII, fig. 10, represents part of a transverse section through the fore part of the head of a duck embryo towards the end of the fourth day. This figure, which is repeated with slight alterations from a former paper,[3] happens to show the points to which I wish to call attention rather better than any of my chick preparations, the specimen from which

[1] 'Quarterly Journal of Microscopical Science,' January 1878, pp. 17—23. To avoid repetition, I beg to refer the reader to the detailed account of the early stages contained in this paper.

[2] I take this opportunity to make a slight alteration in the nomenclature adopted in my former paper. I have there suggested the term *neural ridge* for the longitudinal ridge of cells which grows out from the re-entering angle between the external epiblast and the neural canal, and from which the nerves, whether cranial or spinal, arise. Since this ridge appears before closure of the neural canal is effected, there are manifestly *two* neural ridges, one on either side; but I have also applied the same term, *neural ridge*, to the single outgrowth formed by the fusion of the neural ridges of the two sides after complete closure of the neural canal is effected, and after the external epiblast has become completely separated from the neural canal. I propose in future to speak of this single median outgrowth as the *neural crest*, limiting the term *neural ridge* to the former acceptation. Thus, while there are two neural ridges, there is only one neural crest, a distinction that will be at once evident on reference to my former figures.

[3] 'Journal of Anatomy and Physiology,' vol. xi, plate xxi, fig. 13.

it was taken being in unusually good preservation. The section passes through the forebrain (*f. b.*), the olfactory pit (*olf.*), and the olfactory nerve (1). From it we learn (1) that the olfactory nerves exist prior to the cerebral hemispheres, of which latter there is in this specimen no trace whatever; (2) that in this stage there is no indication whatever of an olfactory lobe; (3) that the olfactory nerve is in its early stages connected with the upper or dorsal part of the side of the forebrain;[1] (4) that the connection between the olfactory nerve and olfactory pit is very early acquired; (5) that the olfactory nerve at this stage agrees closely in histological characters with the corresponding stages of the other cranial nerves, consisting almost entirely of roundish or oval nucleated cells with few or no nerve fibres.

This figure may be advantageously compared with fig. 19, which represents, as already described, a section through the same region in a dogfish embryo at stage M. The resemblance between these two figures is indeed very striking, and extends even to the minute histological details. I would lay great stress on this resemblance, and submit that this close correspondence, amounting almost to identity, in the condition of the olfactory nerve at similar stages in two vertebrates so widely separated as the chick and the dogfish, affords very strong evidence in favour of the correctness of my observations. Such differences as do exist are of very minor importance. Apart from the slight difference in general configuration, the most significant are the rather larger relative size of the olfactory nerve and pit in the dogfish, obviously correlated with their condition in the adult, and the fact that in the duck the attachment of the olfactory nerve is rather nearer to the summit of the forebrain than in the corresponding stage of the dogfish.

The appearance of the cerebral hemispheres towards the close of the third day in the chick causes considerable alteration in the position and relations of the olfactory nerves. The hemispheres are lateral outgrowths of the forebrain, and are from the first situated on the dorsal side of the roots of the olfactory nerves. They grow forwards and upwards with exceeding rapidity, and by so doing drive the olfactory nerves down to the base of the brain, and so cause these nerves to appear to arise from their under and anterior part; a change

[1] Though the nerve is in close contact with the brain, the actual connection between the two is not seen in the specimen figured; it is clearly visible in one of the sections of the same series immediately adjacent, which, however, does not show the whole length of the nerve, and is, therefore, less suitable for figuring.

which has proved a fruitful source of misconception as to the true nature and relations of the olfactory nerves, especially as these latter are usually not recognised *until* they have taken up this secondary position.

The change to which I have just referred is well illustrated by fig. 11, a transverse section through the anterior part of the head of a chick embryo at the eightieth hour. The section shows the commencing cerebral hemispheres (*c. h.*) growing upwards and outwards from the forebrain; it also passes through the margins of the two olfactory pits (*olf.*), and on the left side through the root of the olfactory nerve (1) at its point of origin from the brain; the figure shows very clearly the effect of the appearance of the cerebral hemispheres on the position of the olfactory nerves, and shows further how the secondary connection of these nerves with the hemispheres is acquired.

Fig. 12 represents a section from the same series as fig. 11, but taken a little further back, passing through the olfactory pits (*olf.*) at their deepest parts. On the right side the section passes through the distal portion of the olfactory nerve (1), which is seen to be in continuity with the bottom of the olfactory pit.

In figs. 11 and 12 the olfactory nerve has the same histological character as in fig 10; it is, however, relatively, if not indeed absolutely, smaller than at the earlier period. The figures further show clearly that there is as yet no trace whatever of an olfactory lobe.

I have elsewhere[1] given figures and description of the condition of the olfactory nerves at the ninety-third hour in the chick, at which date, excepting a general increase in size, their condition differs but little from that at the eightieth hour.

Figs. 7 and 8 represent longitudinal and vertical sections through the anterior part of the head of a chick embryo towards the end of the sixth day of incubation. As the olfactory nerve did not lie exactly in the plane of section it has been necessary to figure two sections, of which the more superficial one (fig. 7) shows the greater part of the length and the peripheral distribution of the olfactory nerve; while the second section (fig. 8), taken at a slightly deeper level, shows the root of origin of the nerve from the brain. The olfactory nerve, which is still short, presents a proximal ganglionic swelling at its point of origin from the hemisphere, seen best in fig. 8; along the greater part of its length the nerve consists of very elongated fusiform cells, with a few

[1] Loc. cit., p. 20, and Plate II, figs. 17—19.

spherical ganglionic cells at intervals; distally, at its connection with the olfactory pit, it presents a second ganglionic swelling, fig. 7.

A point of very considerable interest, shown in the clearest possible manner by these figures, is that up to this date there is no indication of an olfactory lobe; indeed, instead of a hollow process of the hemisphere at the point of origin of the olfactory nerve, there is at this point, as is shown by both figures, but especially by fig. 8, a slight external depression, with a very obvious internal projection of the wall of the hemisphere.

Fig. 9 represents a similar section, in a longitudinal and vertical plane, through the nasal region of a chick at the end of the seventh day; passing through the cerebral hemisphere (*c. h.*), the eye (*o. c.*), the anterior extremity of the ophthalmic branch of the fifth nerve (v. *a.*), the olfactory pit (*olf.*), and the olfactory nerve (1). The nerve itself presents the same histological characters as in fig. 7, *i. e.* a proximal ganglionic enlargement at its root of origin, a trunk consisting mainly of nerve fibres, but with a few ganglionic cells at intervals along its whole length, and a distal ganglionic expansion at its point of fusion with the olfactory epithelium. There is, however, one important difference between this figure and the two preceding ones; opposite the point of origin of the olfactory nerve there is a small conical depression (*ol. v.*) of the inner wall of the cerebral hemisphere. From a comparison with fig. 20 there can be little doubt that this is the earliest appearance of an olfactory lobe. As in the dogfish, this lobe is formed at first entirely at the expense of the inner wall of the hemisphere, there being as yet no perceptible projection on the exterior of the brain.

The olfactory lobes, after their first appearance, grow rapidly. By the twelfth day they form a pair of small conical processes, about 1 millimètre in length, springing from the extreme anterior ends of the cerebral hemispheres: the two lobes lie side by side, their apposed surfaces being slightly flattened. Each lobe contains a prolongation of the ventricular cavity of the corresponding hemisphere.

Fig 36 represents a longitudinal and vertical section through the olfactory lobe and the anterior part of the cerebral hemisphere of a twelfth day chick embryo: it shows how the ventricle of the hemisphere (*c.h.*) is prolonged to the extremity of the olfactory lobe (*ol.v.*); and also the mode in which the olfactory nerve arises from the end of the olfactory lobe as a series of bundles of nerve fibres.

Fig. 37 is a transverse section through the olfactory nerve

of a chick embryo of the same age as fig. 36; it shows the bundles of nerve fibres, bound together by connective tissue, which together constitute the olfactory nerve; it shows also how the majority of these bundles are arranged in a circle round the margin of the nerve, while a few smaller bundles lie in the centre.

Figs. 38 and 39 represent sections taken from the same embryo as the preceding figure. Fig. 38 is a transverse section through the olfactory lobe, and shows the laterally compressed ventricular cavity. Fig. 39 is a transverse section through the anterior part of the hemisphere: the outer wall of the hemisphere is seen to have increased greatly in thickness while the inner wall still remains thin; so that the ventricle, which is greatly compressed laterally, no longer occupies the centre of the hemisphere, but lies close to its inner side.

In the adult fowl the olfactory lobe has much the same appearance as at the twelfth day: it is about two and a half millimètres in length, and still contains a central cavity, though this latter is relatively smaller than at the earlier date; the relations of the olfactory nerve to the lobe are the same as at the twelfth day.

In my former paper I stated that *there is no trace of an olfactory vesicle at any period in the life of a chick.*[1] This statement my later work now shows to be erroneous; the chick has an olfactory vesicle, but, as in the dogfish, this vesicle does not appear till an exceedingly late period of development.

The principal points then, in the development of the olfactory nerves in the chick to which I desire to direct attention are:

1. The olfactory nerves arise from the forebrain, before the cerebral hemispheres have begun to be developed.

2. They are at first connected with the dorsal surface of the forebrain, but on the appearance of the hemispheres become driven down to the ventral surface of the brain, and acquire a secondary connection with these latter.

3. From their earliest appearance the olfactory nerves are solid, and present the same histological characters as the other cranial nerves.

4. There is not the slightest indication of an olfactory lobe till the latter part of the seventh day of incubation.

Though these conclusions are in complete accordance with my earlier work, they are directly opposed to all other accounts with which I am acquainted, with one solitary exception, to which I shall refer immediately. As the date

[1] Loc. cit., p. 20.

of appearance of the olfactory lobe is the point in which there is the greatest discrepancy between the descriptions of previous writers and my own, I have made sections in very various planes in order to detect any appearance that could possibly be interpreted as an olfactory lobe at an earlier date than the seventh day, but have failed completely to observe any such.

As far as I can ascertain, the earliest account of the development of the olfactory nerve is that given by Remak; this description, which only occupies about three lines, and is unsupported by figures, is as follows:—"An ihrem Boden (Hemisphären) zeigen sich gegen das Ende des dritten Tages jederseits kleine birnförmige Bläschen (Geruchsbläschen) über deren weiter entwickelung ich keine Beobachtungen besitze."[1] This observation was repeated later on by von Baer, who, however, went further than Remak, and described this vesicle as the rudiment of the olfactory nerve; he also described an olfactory pit distinct from this vesicle. Concerning these statements Remak speaks thus:—"Halte ich diese Angaben mit meinen eigenen Wahrnehmungen zusammen, so wird es mir sehr wahrscheinlich, dass Baer am vierten Tage die Geruchsbläschen und die Nasengruben nicht gleichzeitig beobachtet, dass er vielmehr dasselbe Gebilde bald als Anlage des Riechnerven, bald als Nasengrube gedeutet hat. Ich habe mich nämlich überzeugt, dass die Geruchsbläschen, die zu Ende des dritten Tages auftreten, die nasengruben sind, und dass weder alsdann, noch bis zum fünften Tagen ein entsprechender Auswuchs des vorderhirnes wahrzunehmen ist."[2] This very definite statement shows with perfect clearness not only that Remak recognised and corrected his original mistake, recognised, *i. e.* that what he had originally taken for outgrowths of the cerebral hemispheres were really the olfactory pits, a mistake doubtless due to his relying on surface view of whole embryos; but also that he discovered and recorded the fact that as late as the end of the fifth day there is no trace of an olfactory lobe.

Strange as it may seem, this exceedingly definite and accurate statement of Remak's has been completely overlooked, while his earlier, vague, brief, and avowedly imperfect observation actually furnishes the basis of the descriptions of the development of the olfactory nerve given in our text-books of embryology at the present day.

Thus, Professor Kölliker, in the second part of his text-

[1] 'Untersuchungen über die Entwickelung der Wirbelthiere.' Berlin, 1855, p. 33.

[2] Loc. cit., p. 74, note 55.

book of embryology, published in the course of the present year, dismisses my previous account of the development of the olfactory nerve as "eine Angabe, die mit der Darstellung von Remak, der zufolge die *Lobi olfactorii* des Hühnchens am Ende des zz. Tages als kleine birnförmige Bläschen am Boden der Hemisphärenblasen liegen, nicht zu vereinen ist."[1] Professor Kölliker's words show, beyond doubt, that he is quoting from Remak's earlier statement; had he been acquainted with the latter part of Remak's work he would have known that my observations confirmed instead of contradicting Remak.

Again, Foster and Balfour describe the development of the olfactory nerve in the chick thus:—"At the under surface of each of the vesicles of the cerebral hemispheres there appears towards the end of the third day a small, somewhat elongated vesicle—the *olfactory vesicle*—which is the rudiment of the olfactory nerve or bulb."[2] The authors make this statement on their own authority, but since the first part of their description is an almost literal translation of Remak's earlier account, it is, I think, a fair inference that they have fallen into the same error as Professor Kölliker. Remak, however, is not responsible for the statement that this *olfactory vesicle* is "the rudiment of the olfactory nerve or bulb."

Any further discussion of the literature of this subject would be unprofitable; it is, however, only fair to add that at the time of writing my previous paper I had not referred to Remak's work, and was under the impression that my description was completely at variance with his account; it is, therefore, a matter of great satisfaction to myself to find my statements corroborated by such high authority.

c. In the salmon and trout.—Though my observations on Teleostean embryos are not nearly so complete as those I have just recorded concerning the chick and dogfish, yet, inasmuch as they have yielded definite, and in some respects important and unexpected results, I have thought it well to record them here.

The ova were obtained in the early part of last year from Mr. Capel, of the Foot's Cray Fishery; for the opportunity of hatching them I am indebted to Mr. F. Buckland, to whom my best thanks are due for the liberal and courteous manner in which he met my requests. I am also much

[1] Kölliker, 'Entwickelungsgeschichte des Menschen und der höheren Thiere;' Zweite Auflage. Zweite Hälfte, 1879, p. 609.

[2] 'Elements of Embryology.' Part 1, 1874, p. 117.

indebted to Mr. Edon, of the South Kensington Museum of Pisciculture, to whose care and experience I owe the successful hatching of the ova.

The early stages of development of the olfactory nerve are unfortunately even more difficult to investigate in Teleosteans than in either the chick or dogfish; and my observations on these stages are exceedingly imperfect. The earliest stage at which I can speak with any confidence as to the existence of an olfactory nerve is shown in fig. 29, which represents a transverse section through the anterior part of the head of a trout embryo on the twenty-seventh day after the fertilization of the ova. The section passes through the forebrain (*f. b.*), and through the olfactory pits (*olf.*); on the left side of the section a small mass of cells, somewhat more compactly arranged and more deeply stained than the mesoblast cells, connects the upper part of the forebrain with the olfactory pit. This mass of cells (1) I believe to be the olfactory nerve, mainly from its relation to what is undoubtedly the olfactory nerve a few days later. I do not wish, however, to speak at all positively on this point.

Between the thirtieth and fortieth days the olfactory nerves, though still extremely short, can be easily recognised. Though my observations are far from complete, they suffice to establish the following points for both the salmon and trout:

1. The olfactory nerves appear before the cerebral hemispheres, and are at first connected with the dorsal side of the forebrain.

2. The nerves are, from the earliest period at which their existence can be determined with anything like certainty, solid; *i.e.* there is no olfactory lobe.

3. The connection between the olfactory nerve and the epithelium of the olfactory pit is acquired at a very early date.

Plate XIV, fig. 33, is taken from a transverse section through the head of a salmon embryo two days after hatching. The section, which is a little oblique, passes on the left side through the eye (*o. c.*) with the superior (*r. s.*) and inferior (*r. i.*) recti muscles; on the right side through the olfactory pit (*olf.*) The forebrain (*f. b.*), which lies in the centre of the section, is seen to have a small vesicular cavity in its upper part; its roof is thin, its floor and sides very thick. From the lower part of its sides a pair of nerves (1) arises; these nerves run downwards for a short distance towards the ventral surface, then turn directly outwards, and the nerve on the right side is seen to divide into two branches, which can be readily traced to the thickened

epithelium lining the bottom of the olfactory pit (*olf.*). It will be noticed that there is no trace of an olfactory lobe, and that the olfactory nerve presents no ganglionic enlargement at any part of its course. In its general relations, mode of origin, and course, the nerve agrees remarkably closely with the other cranial nerves, while in histological characters it is identical with them.

In fig. 34 the olfactory nerve (I) is seen in longitudinal and vertical section in a salmon embryo of the same age as that just described. This section shows well the relations of the olfactory nerve to the brain; it also shows the roots of the optic nerves (II), the infundibulum (*inf.*), and the *trabeculæ cranii* (*tr.*).

It would seem, therefore, that if an olfactory lobe is present at any period in the life of a salmon or trout, it does not make its appearance till very late—so late, indeed, that it could have no claim to be considered as an embryonic structure at all: there is no trace of it at the time of hatching, or, indeed for some days afterwards.

d. In other vertebrates.—In the Axolotl[1] the olfactory nerve is at first connected with the forebrain, not with the hemispheres. Throughout the whole period of embryonic development it is very short, and in the early stages exceedingly so: it is solid, and agrees completely in histological characters with the other cranial nerves. I have failed to detect an olfactory lobe in any of the stages I have examined; *i.e.* up to the time of hatching.

I have also made some observations on the earlier stages of development of the olfactory nerves in the frog, which show that in these stages the nerves are extremely short, and that there is no trace of an olfactory lobe. The resemblance between the frog and axolotl is, as might be expected, exceedingly close.

In some lizard embryos, for which I am indebted to Mr. Balfour, I have noticed the existence of solid olfactory nerves, with no indication of olfactory lobes, at stages apparently corresponding to the fourth or fifth day of incubation of the chick; and I believe I have succeeded in establishing the existence of olfactory nerves at still earlier stages, before the appearance of the cerebral hemispheres. In the later stages the olfactory lobes are more prominent objects than in the chick.

I will, in conclusion, quote from Professor Parker the fol-

[1] For the opportunity of investigating the development of the Axolotl, I am again indebted to Mr. Edon, of the South Kensington Museum.

lowing description of the development of the olfactory nerve in the green turtle:—"In embryos of the green turtle of the size of a horse-bean I find the nerves (olfactory) solid. When the embryos are two or three times that size, these nerves each acquire a large cavity proximally, from the fore wall of which the branches seem to spring. The foremost of these branches spring from the top of the vesicle; they arose at first from the top of the forebrain."[1]

e. General considerations.—Before proceeding to the development of the olfactory organ, I propose to summarise the results to which we have already been led, and to consider briefly certain questions of a more theoretical character.

The first point I desire to call attention to is the remarkably close agreement in the mode of development of the olfactory nerves presented by the several types examined, types which, it will be noticed, embrace examples from each of the vertebrate classes, with the exception of Mammalia. In all these types alike—dogfish, trout and salmon, axolotl, frog, lizard, turtle and chick—the mode of development is fundamentally the same; while the resemblance between the dogfish and the chick, the most generalised and the most specialised of these types is, as I have already shown, complete. I would direct special attention to this agreement as affording very strong testimony of the correctness of my observations.

The fundamental points common to all the above types are the following:—1, the olfactory nerves appear very early; 2, they are at first connected with the forebrain, and not with the cerebral hemispheres; 3, they are solid, and agree completely in histological characters with the other cranial nerves; 4, an olfactory lobe, when present at all, does not appear till an exceedingly late period of development.

Though the several types agree so closely in the above fundamental points, they present well-marked differences among themselves. The dogfish appear to form a central type round which the others may be grouped, and from which they may be supposed to be derived. Curiously enough, of the other types the chick appears to resemble the dogfish more closely than any of the others do, with the possible exception of the lizard and turtle, whose earlier stages are as yet unknown. The Amphibia are chiefly characterised by the extreme and long persisting shortness of their olfactory

[1] "On the Development of the Skull and its nerves in the Green Turtle (*Chelone Midas*)." 'Proc. Royal Society,' 1879.

nerves, and are in no way intermediate between the dogfish and such Sauropsida as I have examined. Finally, the Teleosteans, if the salmon and trout may be taken as typical of that group, while they resemble the Amphibia in the extreme shortness of their olfactory nerves in the early stages of development, seem to differ somewhat from the other types in the exceedingly late appearance of the olfactory lobes, and in the striking resemblance in general anatomical behaviour between the olfactory and the other cranial nerves.

The nomenclature of the olfactory nerve is, unfortunately, somewhat overburdened with synonyms, a never-failing source of confusion and inaccuracy. The "olfactory nerve" of an adult vertebrate is, perhaps, best described as consisting of three parts; a proximal *tractus olfactorius* arising from the cerebral hemisphere, an intermediate ganglionic enlargement or *bulbus olfactorius*, from whose distal extremity the third part or *nervus olfactorius* arises.[1] Of these parts the two former are commonly and correctly described as being properly parts of the brain, and as together constituting the *rhinencephalon*. By some authors, however, the term rhinencephalon appears to be limited to the bulbus olfactorius, the tractus olfactorius being then spoken of as the *rhinencephalic crus*.[2] By *olfactory lobe* or *olfactory vesicle* is usually meant the hollow diverticulum of the forebrain or cerebral hemisphere in the embryo, from which both the *tractus olfactorius* and *bulbus olfactorius* of the adult are developed, and which has hitherto been erroneously supposed to be the earliest part of the "olfactory nerve" to be developed. It would, perhaps, be well to limit the term *olfactory lobe* to this embryonic structure; Owen employs it in the adult as synonymous with *bulbus olfactorius*.

From the descriptions I have already given it follows that the *nervus olfactorius* is the earliest of the three elements to be developed, and that it alone is the direct homologue of the other cranial nerves. The term *olfactory nerve* ought then to be strictly limited to the *nervus olfactorius*. Since, however, there is considerable inconvenience in disturbing established nomenclatures, it may perhaps be well to continue to use the term *olfactory nerve* in the ordinary anatomical sense, and to confine oneself to the term *nervus*

[1] *Vide* Max Schultze. "Untersuchungen über den Bau der Nasenschleimhaut bei dem Menschen und Wirbelthiere." Halle, 1862, pp. 18, 19; and Stannius, 'Handbuch der Anatomie der Wirbelthiere,' 2 Auflage, 1854, p. 165, seq.

[2] Owen, 'Anatomy of Vertebrates,' vol i, p. 283, 1866.

olfactorius when wishing to speak of the third or distal element, the *olfactory nerve proper;* in this case, however, it must be clearly understood that *olfactory nerve* and *nervus olfactorius* are by no means equivalent or mutually convertible terms.[1]

Though the *bulbus olfactorius* and *tractus olfactorius* are considered as together equivalent to the *olfactory lobe* of the embryo, it must be noticed that the proximal ganglion of the *nervus olfactorius* may fuse so completely with the *bulbus*, that it is, even in comparatively early stages, "rather difficult to fix on the exact line of demarcation between the bulb and the nerve."[2]

The three elements of the olfactory nerve, but especially the first and third, vary much in the relative proportions they attain in the adult. Thus, in the dogfish there is a large bulbus olfactorius, connected proximally with the hemispheres by a short, thick, tractus olfactorius, and giving origin distally to the numerous filaments of the nervus olfactorius. In the skate, while the bulbus and nervus retain much the same proportions as in the dogfish, the tractus olfactorius is of very great length. Among osseous fishes the variations are still greater; in the pike, salmon, perch, gurnard, &c., on the one hand, there is a very long nervus olfactorius, springing from a bulbus olfactorius which is in close contact with the hemispheres; on the other hand, in the cod, carp, &c., as in the skate, the bulbus olfactorius is situated near the olfactory organ, and is far removed from the rest of the brain, with which it is connected by a long tractus olfactorius.

A question of far more morphological interest is the relation of the olfactory nerve to the other cranial nerves. My observations, if confirmed, prove that in the chick up to the end of the sixth day, in the dogfish up to stage o, and in the salmon and trout, at any rate up to the time of hatching, the olfactory nerve agrees very closely in histological characters and in general anatomical relations with the other cranial nerves. I propose now to consider these resemblances more in detail, and specially in reference to the question of the segmental value of the olfactory nerve.

Certain of the cranial nerves—*e. g.* the facial and glossopharyngeal—have long been acknowledged to possess segmental value. If we consider the mode of development of these segmental cranial nerves, we find that they agree among themselves, and differ sharply from other nerves

[1] *Vide* 'Quain's Anatomy,' 8th edition, vol. i, p. 526.
[2] Balfour, op. cit., p. 178.

or branches of nerves in the following embryological characters:

1. They appear very early.

2. They arise, at least in the chick, from the neural crest on the mid-dorsal surface of the brain.

3. Shortly after their appearance their roots undergo a shifting downward of their points of attachment, so that they no longer arise from the dorsal surface, but from the sides of the brain.

4. They present, at least in their early stages, ganglionic enlargements on or close to their roots of origin.

5. Their course is at right angles to the longitudinal axis of the head.

6. Finally, they have very definite relations to the segments of the head, as indicated by the visceral clefts, each nerve supplying the two sides of a cleft.

The true cranial segmental nerves, such as the facial and the glosso-pharyngeal, agree in presenting all these characters. On the other hand, the non-segmental nerves, or branches of nerves, though they may possess some of the characters above enumerated, yet never present all, and rarely more than one or two. This test suffices to dispose of the claims to segmental rank of the optic, the auditory, the fourth, and sixth nerves, and of the ophthalmic branch of the trigeminal nerve; while, on the other hand, it serves to demonstrate the segmental value of the third nerve.

I propose now to apply this test to the olfactory nerve.

1. In all the types examined the olfactory nerve appears very early. Though the exact date of its first appearance has not been determined with certainty in any case, yet there is no reason for thinking that it arises later than the other cranial nerves. In all the types considered it appears before the cerebral hemispheres.[1] In the dogfish it makes its appearance earlier than stage K, and in the chick there are strong reasons for thinking that it is "one of the first nerves in the body to appear."[2]

2. I have already attempted elsewhere to prove that in the chick the olfactory nerve is developed from the neural crest.[3]

[1] Though I have but little doubt on the matter myself, I have not yet succeeded in determining this point with absolute certainty in the case of the lizard.

[2] 'Quarterly Journal Microscopical Science,' Jan., 1878, p. 23.

[3] Loc. cit., pp. 17—19. With reference to the extension forward of the neural crest in the chick to the forebrain, Prof. Kölliker suggests (op. cit., pp. 661—2), that I have been misled by certain folds which appear during closure of the medullary canal, and to which His has already directed attention. With all due respect for Prof. Kölliker's authority, I cannot

I have nothing to add to the arguments already given, though I am fully aware that the point is not yet proved. In the Elasmobranchs, the only other vertebrates in which the presence of a neural crest has been accurately described,[1] the anterior limits of this crest have not been fixed with certainty.

3. The shifting down of their roots of origin, one of the most striking features of the segmental nerves, is a very constant and well-marked point in the development of the olfactory nerves. It is well shown for birds in figs. 10 and 11, and for the dogfish in figs. 19 and 20. In the dogfish the displacement of the roots is less extensive than in the chick—a point obviously correlated with the greater development of the cerebral hemispheres in the latter.

4. The course of the segmental nerves in their early stages is, speaking within certain limits, at right angles to the longitudinal axis of the head at their point of origin. The facial and the postauditory nerves arise from a part of the head in which this axis is a straight line; the nerves consequently run parallel to one another, as is seen in figs. 4 and 6. In front of the origin of the facial nerve the axis of the head is, owing to cranial flexure, no longer a straight line, but a curved one. The trigeminal nerve is disturbed only to a very slight extent, but it will be seen in fig. 4 that instead of running parallel to the facial, the two nerves converge slightly towards their distal ends. In the region of the midbrain the effects of cranial flexure are very well marked; but fig. 6 shows that the course of the third nerve, the segmental nerve arising from the midbrain, is still at right angles to the longitudinal axis at its point of origin. Since the direction of the axis at this point is almost at right angles to its original direction, so also the third nerve is seen to take a course almost at right angles to the facial or glosso-pharyngeal. Similarly, the course of the olfactory nerve is at right angles to the longitudinal axis of the head at its point of origin; and its direction is such that if cranial flexure were corrected and the head straightened out the olfactory nerve would run parallel to the third, trigemi-

accept this explanation. My specimens leave no room for doubt that whatever may be its morphological importance, the neural crest is a perfectly continuous structure, extending in the chick at the twenty-ninth hour from the anterior end of the optic vesicles nearly to the end of the hindbrain. I am acquainted with folds such as Prof. Kölliker describes, but have only met with them in imperfectly-prepared specimens, and especially in specimens hardened in chromic acid, which, in my hands, at least, has always proved a peculiarly unreliable hardening agent.

[1] Balfour, 'Elasmobranch Fishes,' pp. 191, 192.

nal, facial, and other segmental nerves. I have investigated very carefully this point, which I am disposed to regard as of some importance, and find that in the chick, at a time when cranial flexure has attained its maximum development, the angle formed by producing the direction of the olfactory nerve and of the facial or glosso-pharyngeal nerves until they meet, is almost identical with that which measures the amount of cranial flexure; the angle in either case being about 120°. The course of the olfactory nerve in dogfish embryos is shown in figs. 17 and 18, and in the salmon in figs. 33 and 34.

5. This is a point of comparatively little importance, inasmuch as in the embryo ganglia, or local accumulations of nerve-cells, appear to be developed in a very irregular manner, and at very various points in the course of the nerves. Still it is a point not altogether destitute of weight, since those cranial nerves which appear for other reasons to have no claim to rank as segmental, are also peculiar in not possessing ganglionic enlargements at or near their roots of origin in the early stages. In the chick these ganglia are shown for the olfactory nerves in figs. 7, 8, and 9; for the third nerve in fig. 6; and for the trigeminal in fig. 4. In the dogfish the ganglia of the olfactory nerves are shown in figs. 20 and 21.

6. The discussion of the question whether the olfactory nerve is related to a visceral cleft in the same manner as the segmental nerves are to their respective clefts, will find a more suitable place after the development of the olfactory organ has been considered.

The distance between the root of the fifth nerve and that of the third is somewhat greater than that between the fifth and the facial, while that between the third and the olfactory is greater still. These facts, which are obviously correlated with the great hypertrophy of the anterior part of the brain, from which the nerves in question spring, can certainly not be used as arguments against the segmental nature of the olfactory nerve.

Though the olfactory nerve, from the earliest period at which it is recognisable as such, is thus seen to agree with the segmental nerves in all essential characters, it yet presents one or two minor points of difference. In the first place, owing to the close proximity of the forebrain to the nasal pit, the olfactory nerve is shorter than the other cranial nerves at the same age. Secondly, the olfactory appears to lag behind the others in development; thus, at a time when the other nerves are fibrillar along the greater part of

their length, and only present nerve cells in any considerable number at certain points, the olfactory nerve still presents nerve-cells along its whole length. This second difference appears, however, to depend on the first, since as the nerve elongates with age, we find it gradually taking on the histological characters of the other nerves, *i. e.* the greater part of its length becomes fibrillar, and the nerve-cells confined to the two extremities, where they form ganglionic swellings. The practical importance of these differences is, however, considerable, since, owing to the olfactory nerve consisting for some time after its first appearance almost entirely of rounded cells, it is very difficult to distinguish from the surrounding mesoblast, and may, therefore, very readily be overlooked.

The olfactory nerves are by most authors considered as of totally different morphological value to the other cranial nerves.

According to Gegenbaur, "the cerebral nerves . . . . . are seen to break up into two very distinctly marked divisions, when examined after the comparative method. One division, the larger, contains nerves which more or less agree with, or might even be derived from, spinal nerves, while the other contains *those which have not the faintest resemblance to spinal nerves.* This latter divison contains two specific sensory nerves, the olfactory and the optic."[1]

Again, Prof. Huxley says, "The greatest number of pairs of nerves ever given off from the vertebrate brain is twelve, including the so-called olfactory nerves and the optic nerves, which, as has been seen, are *more properly diverticula of the brain than nerves in the proper sense of the word.* The olfactory 'nerves' (*olfactorii*) constitute the *first pair* of cerebral nerves. They always retain their *primary connection with the cerebral hemispheres,* and frequently contain, throughout life, a cavity, the *olfactory ventricle,* which communicates with the lateral ventricle."[2]

Finally, Balfour considers that the "very late appearance and peculiar relations" of the olfactory nerve "are, at least for the present, to my mind sufficient grounds for excluding it from the category of segmental cranial nerves."[3]

I have already attempted to show that the existence of an olfactory lobe or vesicle can in no way be said to militate against the establishment of a complete homology

[1] 'Elements of Comparative Anatomy,' English translation, p. 515. The italics are mine.

[2] 'Anatomy of Vertebrated Animals,' p. 71. The italics again are mine.

[3] Op. cit., p. 215.

between the olfactory and the other cranial nerves. A structure that does not make the slightest appearance till the seventh day in the chick and stage o in the dogfish; a structure that, in the chick, does not appear till long after the nerves have acquired their connection with the cerebral hemispheres, a connection which I must repeat is a purely secondary one, and not, as Prof. Huxley would have it, primary; such a structure can hardly be deemed of sufficient morphological importance to outweigh the very obvious and striking resemblances between the olfactory and the other cranial nerves to which I have already referred.

Again, if my observations are correct, the olfactory nerves cannot be said to appear "very late;" while, if I may assume that I have fairly disposed of the olfactory vesicle difficulty, I fail to see what are the "peculiar relations" of the olfactory nerve that would justify its exclusion "from the category of segmental cranial nerves."

The condition of the central nervous system appears to me to afford evidence of some value in favour of the segmental nature of the olfactory nerve. There is certainly no obvious reason why the anterior cerebral vesicle, or forebrain, of the embryo should be considered to be of a different nature to the middle cerebral vesicle, or midbrain, or to any one of the vesicles of the hindbrain. The early embryonic stages afford no evidence whatever of a break of any kind between the fore and midbrains; and, if the nerves arising from the mid and hindbrains have segmental value, there is surely a presumption in favour of the nerve that takes its origin in the forebrain having a similar and equivalent value; a presumption greatly increased in probability by the close similarity between the early stages of development of that nerve and of the nerves arising further back in the brain.

It still remains to be considered what is the morphological import of the olfactory lobe or vesicle; but this is a question to which, in the present state of our knowledge, any answer that may be given must partake very largely of a speculative nature. The principal facts we have to guide us appear to be:

1. The very late appearance of the olfactory lobe.

2. The fact that though the olfactory lobe is obviously connected with the root of origin of the olfactory nerve, yet it has no relation to the original position of the root of the nerve, and does not appear till this root has acquired a new, and purely secondary position.

3. The fact that the olfactory lobe does not appear at

equivalent periods in the development of different vertebrates. In the dogfish the olfactory lobe appears before the division of the forebrain into cerebral hemispheres takes place; in the chick not till long after the appearance of the cerebral hemispheres; and in the salmon, at any rate, not till after the time of hatching.

These facts would appear to indicate that the olfactory lobe is to be viewed rather as an adult or adaptative than as an embryonic or primitive structure; a view that is materially strengthened by the great variations in relative size of the three elements of the olfactory nerve in various adult vertebrates, to which attention has already been directed.

One of the most remarkable features of the early stages of development of all vertebrates, is the enormous preponderance of the central nervous system to which at first everything appears to be subordinate, and which exercises a most important influence on the shape of the embryo. The rapid growth of the neural surface causes the body to become curved towards the ventral surface; this curvature is naturally most marked at the free extremities of the body, and at the head end is the main, if not the sole, cause of cranial flexure. Owing to this cranial flexure the forebrain gets carried in front of the olfactory sacs, and, consequently, the olfactory nerves, which, as we have seen, acquire their connection with the olfactory sacs at a very early age, at first run in a direction downwards and backwards. *Vide* figs. 2, 15, 17, and 18.

Having attained this enormous relative development the nervous system stops for a while, and the face begins to grow more rapidly, causing the so-called rectification of the cranial flexure; the olfactory sacs get carried further and further forwards, so that the olfactory nerves, instead of running downwards and backwards, now run directly downwards, or downwards and outwards as seen in fig. 33. The face still continuing to grow rapidly, while the brain undergoes little or no increase in length, the olfactory sacs get carried in front of the forebrain, so that the olfactory nerves now run downwards and forwards. A continuation of this process carries the olfactory sacs still further forwards, to an extent varying much in different vertebrates, so that the olfactory nerves ultimately run directly forwards as in most adult vertebrates. *Vide* fig. 36.

All the nerves of the body undergo during their development a considerable lengthening, owing to the gradual separation of their central and peripheral ends; but while in the case of all the other nerves this is a gradual and con-

tinuous process, commencing with their earliest appearance, the olfactory nerves are somewhat peculiarly situated. In their early stages, owing to the close proximity of the olfactory sacs to the brain, the olfactory nerves are exceptionally short; and, owing to their origins being at first further forward than their insertions, the growth forwards of the face, carrying the olfactory sacs with it, does not at first cause any lengthening of the olfactory nerves. It is not till the sacs get in front of the forebrain that any lengthening is necessary, but no sooner does this occur than a sudden call is made on the olfactory nerves, which, previously quiescent, now have to commence growing rapidly in length and to continue so doing.

I would therefore suggest, without wishing to attach too much weight to the suggestion, that this elongation of the olfactory nerve, occurring under these exceptional conditions, may take place partly at the expense of the nerve itself, and partly at the expense of the brain; and that it is in this way that the olfactory lobe is produced. It is certainly worthy of notice that in the two types—chick and dogfish—in which I have ascertained with precision the date of its first appearance, the olfactory vesicle comes into existence just about the time that the most rapid growth of the nose and snout occurs, and consequently just about the time when a sudden and rapid lengthening of the olfactory nerve becomes necessary. It is also a significant fact that the olfactory lobe grows very rapidly at first, the nerve itself remaining nearly stationary.

The above suggestion renders it easily intelligible that much variety should exist as to the relative lengths of the *nervus* and *tractus olfactorius*, even in nearly allied vertebrates; while it is quite possible that, at any rate in some forms, the skeletal elements may have an important share in determining the relative growth of nerve and brain.

II. *The Olfactory Organ.*

a. Development of the olfactory organ.—The consideration of the olfactory nerve having taken up far more space than I had originally anticipated, I shall be compelled to deal with the olfactory organ in a somewhat more summary fashion. The points to which I wish here to call attention are the remarkable resemblances that exist between the olfactory pits and the visceral clefts. As in the first part of the paper I shall deal first with matters of direct observation, and afterwards consider the theoretical side of the subject.

The vertebrate olfactory organs make their first appearance as "a pair of slight thickenings of the external epiblast on the under surface of the forebrain, immediately in front of the mouth. . . . Each thickened patch of skin soon becomes involuted as a shallow pit."[1]

In the dogfish these thickenings appear "during a stage intermediate between L and K" (Balfour). Their condition during stage K is well shown in figs. 13 and 14 (*olf.*); the former figure being a longitudinal and horizontal section, the latter a vertical and transverse one. The exceedingly close proximity of the bottom of the olfactory pit to the brain is well shown by both figures. Fig. 13 shows also that at a time when the nose is in a very rudimentary condition, the eye (*o. c.*) has already made considerable progress in development, a point to which Balfour has already directed attention.

The communication between the visceral clefts and the exterior is established almost simultaneously with the first appearance of the olfactory pits. At stage L there are "three visceral clefts, none of which are as yet open to the exterior."[2] At stage K, according to Balfour, "four visceral clefts are now visible, all of which are open to the exterior, but in a transparent embryo one more, not open to the exterior, would have been visible behind the last of these."[3] The visceral clefts, then, first become open to the exterior between stages L and K, and we have already seen that it is between these same two stages that the thickenings of the epiblast appear which form the earliest rudiments of the olfactory pits.

In the chick the early stages of development of the olfactory pits closely resemble those just described in the dogfish. Fig. 1 represents a longitudinal and horizontal section through the head of a fifty-four hours' chick embryo; the section, which may with advantage be compared with fig. 13, shows on the right side the olfactory pit (*olf.*), formed by the thickened and involuted epiblast, and in close proximity to the forebrain (*f. b.*); on the left side the section, which is a little oblique, passes through the thickened epiblast forming the margin of the olfactory pit, and through the eye (*o. c.*). Two visceral clefts (*v. c.*) are shown, both open to the exterior.

The earliest period in the chick at which I have noticed the thickening of the olfactory epithelium is about the

[1] Balfour, op. cit., p. 184.
[2] Balfour, op. cit., p. 77.
[3] Op. cit., p. 78.

forty-eighth hour; a period almost identical, as in the dogfish, with the opening of the visceral clefts to the exterior.

In the trout the mode of development of the olfactory pits corresponds very closely with that occurring in the chick and dogfish; and, as in these two types, their first appearance coincides almost exactly with the opening of the visceral clefts to the exterior.

The connection between the olfactory nerve and the bottom of the olfactory pit is, as already noticed, acquired exceedingly early, very shortly indeed after the appearance of the latter. The condition of the olfactory organ in the dogfish is shown at stage M in figs. 15, 16, and 19; and at stage O in figs. 17, 18, and 20. In the chick the olfactory organ is shown at the sixty-fourth hour in fig. 2, at the sixty-seventh in fig. 3, and at the ninety-sixth hour in figs. 5 and 6.

Throughout their early stages of development the olfactory organs present a striking resemblance to the visceral clefts, both in form, position, and general relations—a resemblance which it will be necessary to consider in some detail, inasmuch as it has been very generally overlooked hitherto.

Fig. 3 represents a longitudinal and vertical section through the head of a chick embryo at the sixty-seventh hour. The section, which is taken in a plane not far from the surface, passes through the hind, mid, and forebrains, through the auditory vesicle (*aud.*), the eye (*o.c.*), the trigeminal (V), and auditory (VIII) nerves, through the anterior visceral clefts and arches, and through the olfactory pit (*olf.*). The olfactory pit is seen to bear a marked resemblance to the visceral clefts: like them it is situated on the ventral surface of the head; it is open below; its axis is at right angles to the longitudinal axis of the head, so that were the head straightened out it would be parallel to the clefts; and its general appearance and relations are such as to strongly suggest the view that it is one of the same series of structures as the visceral clefts. It is indeed separated from the next cleft, that in front of the maxillary arch (*Mx.*), by an interval somewhat greater than that separating the hinder arches from one another; but when we consider the enormous hypertrophy which the part of the brain with which it is connected has undergone, this becomes rather an argument in favour of than against the comparison.

Figs. 4, 5, and 6 are three sections taken from the same embryo, a ninety-six hours' chick. Of these sections, which are taken in a longitudinal vertical plane, that given in fig. 4 is the most superficial, that in fig. 6 the deepest of the

three. Figs. 5 and 6 are drawn from consecutive sections, but between figs. 4 and 5 two sections intervened. These figures illustrate well the points to which I have just called attention; they show that the visceral clefts form a continuous series of structures, of which the most anterior is, not the mouth cleft (between *Mn.* and *Mx.*), but the cleft in front of the maxillary arch; a cleft that, following Prof. Parker, I propose to speak of as the lachrymal cleft: they show further that just in front of the lachrymal cleft is the olfactory pit (*olf.*), and that the relations of the pit are such as to inevitably suggest that the olfactory organ is one of the same series of structures as the visceral clefts. Correct the cranial flexure, and straighten out the head, and the resemblance would amount almost to identity. I have only to add that, though these figures are semi-diagrammatical, yet as far as the outlines go, which alone concern us at present, they are as absolutely accurate as I have been able to make them.

The resemblance between the olfactory organ and the visceral clefts is quite as marked in the early stages of the dogfish as in the chick; but to convey anything like an adequate idea of it would require a much more extensive series of figures than I am able to give here.

Fig. 16 is taken from a longitudinal and vertical section through the head of a dogfish embryo at stage M. The section which is taken very near to the surface passes through the auditory vesicle (*aud.*), parts of the trigeminal, facial, auditory, glosso-pharyngeal and vagus nerves, the second head cavity (*h.* 2), the eye (*o.c.*), the mandibular, hyoid, and first four branchial arches, as well as through the olfactory pit (*olf.*). The section is a little deceptive, inasmuch as, owing to the head being somewhat constricted just behind the eyes, the buccal and lachrymal clefts do not appear at all, while the constriction just referred to presents somewhat the appearance of a visceral cleft between the olfactory organ and the mandibular arch, and might possibly be mistaken for one on a superficial examination. The figure illustrates well the resemblance between the olfactory organ, which is larger than at a corresponding stage in the chick, and the visceral clefts.

Fig. 18 shows the same parts in a dogfish embryo of stage O; as in the preceding figure, and for the same cause, the buccal and lachrymal clefts do not appear in the section, but the figure shows the general resemblance in position and relations that exists between the olfactory organ and even the hinder visceral, or branchial, clefts.

In connection with this point, the study of whole embryos affords evidence fully as striking as that yielded by sections. I would here refer especially to certain of the figures given by Professor Parker in his monograph on the "Structure and Development of the Skull in Sharks and Skates," published in the 'Transactions of the Zoological Society' for 1879: on Plate XXXIX side views of the heads of embryos of *Raia maculata* are given (figs. 1 and 2), in which the resemblance between the slit-like aperture of the olfactory organ and the gill slits is shown with remarkable distinctness. The direction of the slit forms an angle of about 120° with the hyomandibular or spiracular cleft, which angle is almost exactly that made by the longitudinal axis of the forebrain with that of the hindbrain, *i.e.* is the amount of cranial flexure; hence, but for cranial flexure, the external slit-like aperture of the olfactory organ would be parallel to the perfectly similar gill slits.

The figures of dogfish embryos of stages K and L, given by Mr. Balfour on Plate VII of his monograph on Elasmobranch Fishes, illustrate the same points. The reference to these two works acquires additional weight from the consideration that the figures which I have named were drawn, I have reason to believe, without the slightest intention on the part of the authors to direct attention to the resemblance. Even in an adult skate the similarity between the olfactory organ and the gill slits is sufficiently striking.

The same points appear, if possible, still more clearly in axolotl and salmon embryos, especially in the former. I have found, however, that to give any adequate representation of these would require a large number of figures, which figures would also serve to illustrate other points in the development of the axolotl, which I hope to deal with on some subsequent occasion.

Fig. 30 represents a longitudinal and vertical section through the head of a trout embryo on the thirtieth day after fertilisation of the ova. The section passes through the hind and midbrains and the eye (*o. c.*). The ventral surface of the section presents a series of undulatory folds, corresponding to the bases of the visceral arches, with their intervening clefts. The olfactory pit (*olf.*) is seen to form the most anterior of these depressions, and to differ from the hinder clefts in little but the greater thickness of its epithelium, and the somewhat greater interval between it and the next cleft. The cleft next but one to the olfactory pit is that over which the trigeminal nerve forks—*i. e.* the buccal or mouth cleft; it is situated between the maxillary

(*Mx.*) and mandibular (*Mn.*) arches. Behind the mandibular arch, between it and the hyoidean arch, is the cleft, the two sides of which are supplied by the facial nerve. Between the buccal cleft and the olfactory pit a cleft intervenes—the lachrymal cleft; so that the number of clefts in the trout agrees completely with that we have already found in the chick.

The resemblances between the olfactory pit and the visceral clefts are, however, not simply those of general appearance and relations; they are of a far more intimate nature, and extend even into the details of histological structure. For studying these more intricate relationships the dogfish has proved the most suitable.

The olfactory organ of a dogfish does not long remain a simple pit; very soon after its first appearance its walls become thrown into a series of folds—the rudiments of the Schneiderian folds of the adult. I wish here to call attention to the resemblances between these folds and the series of folds which, arising from the sides of the visceral clefts, form the rudiments of the gills.

I have not myself observed the presence of the rudimentary Schneiderian folds in embryos younger than stage M, but Balfour has shown that they not only exist, but have acquired the characteristic adult arrangement in embryos "a little older than K."[1] With regard to the gills, Balfour's description is as follows:—"Towards the close of stage K there arise, from the walls of the second, third, and fourth clefts, very small knob-like processes, the rudiments of the external gills. These outgrowths are formed both by the lining of the gill cleft and by the adjoining mesoblast."[2] If, indeed, the times of appearance be not absolutely identical in the two cases, the correspondence is, at any rate, sufficiently striking.

Fig. 23 is a horizontal and longitudinal section through the head of a dogfish embryo at stage N, magnified twenty diameters; it passes through the fore and hind brains, the notochord (*n*), the eyes (*o. c.*), the oculo motor (III) and trigeminal (V) nerves, and through the olfactory pits (*olf.*). The bottoms of these pits are seen to be thrown into a series of small equidistant folds—the Schneiderian folds.

Fig. 24 is a transverse section through the body of the same embryo, taken a short way behind the head, and passing through one of the branchial arches on either side. The section which, like the preceding one, is magnified twenty

[1] Op. cit., p. 184, and Plate XIV, fig. 14.
[2] Op. cit., p. 211.

diameters, shows also the spinal cord, with the anterior and posterior roots of a spinal nerve, the notochord (*n.*), muscle plates (*m. p.*), pharynx (*al.*), parts of the vagus nerve, the cardiac and dorsal aortæ, and on either side the branchial arteries (*b. a.*) The free surface of each branchial arch presents a series of small equidistant folds, the rudiments of the gills (*g.*), which, even under this low magnifying power, have a close resemblance to the Schneiderian folds.

In order to show this resemblance more satisfactorily I have given figures of the parts in question on a larger scale. Fig. 25 represents the right olfactory pit of fig. 23, and fig. 26 the left gill of fig. 24; both figures are thus taken from the same embryo, and the magnifying power employed —ninety diameters—is the same in the two cases.

These figures show that the correspondence between the two structures is by no means confined to their coarser anatomy, but extends even to histological details. The folds are seen to be in the two cases—gills and Schneiderian folds —of the same width, and the same distance apart; in both cases, though consisting mainly of epithelium, they yet involve the underlying mesoblast to a certain, though slight, extent,[1] but as nearly as possible to the same extent in the two cases. The epithelium that forms the greater part of the folds is of the same thickness in the two cases, and of the same histological character, consisting mainly of columnar cells in close contact with one another, and arranged, as a rule, in two rows.

The same folds are shown, at a somewhat later period, in figs. 27 and 28, the former representing the Schneiderian folds, the latter the gills of the same embryo. Though the resemblances are still strong, there are now well-marked differences between the two structures; thus, in fig. 27 the epithelium is somewhat thicker than in the gills, while the mesoblast enters more largely into the gills than the Schneiderian folds. Most of the gill folds already present a central blood-vessel; it is very difficult to satisfy oneself of the existence of distinct walls to these blood-vessels, which appear in many cases to be simply channels in the mesoblast forming the axis or core of each gill fold. Similar blood-vessels exist, especially at a rather later stage, in the Schneiderian folds, and their relations are similar to those in the gills.

Even in adult Elasmobranchs the Schneiderian folds resemble the gills closely in their great vascular supply, in

[1] Balfour notes this in the case of the gills, but describes the Schneiderian folds as folds of epithelium. Op. cit., p. 184.

the arrangement and distribution of the blood-vessels, and in the characters of their surface epithelium.

b. General considerations.—Hitherto we have been concerned simply with matters of observation; though, indeed, I have not attempted to give a complete account of the development of the olfactory organ, but have limited my description to certain developmental features, in which it strongly resembles the visceral clefts; still I have dealt simply with facts, or what I believe to be facts. I propose now to consider the subject from a more theoretical point of view.

In the first place I would submit that the very close resemblance as to form, structure, general relations, time of appearance, &c., existing between the olfactory organ and the gill clefts, whether these be considered as wholes or in their separate parts, is sufficient to raise a strong probability that they are homologous structures.

This probability is strengthened by the complete absence of similar structures in any other part of the body at any period of development. Not only do the Schneiderian folds and the gills appear at the same time and agree completely in structure, but in no other part of the body do similar structures occur, either at this or any other period.

Again, this probability gains very material support from the conclusion arrived at in the first part of this paper, viz. that the olfactory nerve is a segmental nerve; for we have seen that one of the most important diagnostic characters of a segmental nerve is its distribution to the two sides of a visceral cleft, and, since the olfactory nerve is distributed to the olfactory organ, and to that alone, if there be a visceral cleft with which it is in relation, the olfactory organ must be that cleft.

The conclusions, then, to which I have been led concerning the morphology of the vertebrate olfactory organ are—*that the olfactory organ is the most anterior visceral cleft; that the olfactory nerve is the segmental nerve supplying the two sides of that cleft in a manner precisely similar to that in which the hinder clefts are supplied by their respective nerves; and that the Schneiderian folds are homologues of gills.*

The suggestion that the nasal organs are gill clefts was originally made by Dr. Dohrn, in his essay on the origin of vertebrates. In discussing the question whether the pair of gill clefts, which by their median fusion formed the vertebrate mouth, was the most anterior pair, Dr. Dohrn says: "Aber auch betreffs der vorderen Kiemenspalten ist noch

die Vermuthung zu äussern, ob nicht vielleicht in den Nasengruben ein Paar solchen Spalten, freilich in wesentlich veränderter Function und darum auch Structur, zu erkennen sei."[1]

Dr. Dohrn does not enter into any details concerning the suggestion thus made, and does not discuss the question of the olfactory nerve. I am not aware that he has since published any further observations on this point. The suggestion appeared to me, if not untenable, at any rate unprovable, so long as the ordinary account of the development of the olfactory nerve continued to find acceptance.

In addition to what has been already said there are, I think, many arguments in favour of this view. Even if we leave out of consideration the buccal and lachrymal clefts, it is well known that in all vertebrates above Amphioxus more or fewer of the visceral clefts undergo modification to a greater or less extent, and that this modification is first felt by the clefts at the two extremities of the series, especially by the anterior ones; and it is a point worthy of notice that, while the posterior clefts tend simply to disappear, the anterior clefts with their gills are peculiarly prone to persist in a modified form. Thus, the first post-oral or hyomandibular cleft is the only one which remains in Sauropsida and Mammalia. Among Ichthyopsida this cleft is apt to assume the modified form of a spiracle, while its gill loses its respiratory function, and persists as a pseudobranchia. Similarly, the carotid gland of the frog and the choroid gland of Teleosteans are probably other instances of the persistence, in an altered condition, of anterior gills. On the other hand, when reduction is effected in the number of the gills from the posterior end of the series, as in nearly all fishes, the gills and their clefts usually disappear absolutely and completely.

Again, if the olfactory organ is a gill, we should expect to find the resemblance between the two structures strongest in the most primitive vertebrates. From what has been said already this obviously is the case. Of the various types of vertebrates examined it is in the dogfish alone that we find the intimate relation between the development of the gills and that of the Schneiderian folds.

Whatever view we may hold as to the ancestry of vertebrates, there can be little doubt that they have not inherited their olfactory organ as such. At any rate, we know as yet of no invertebrates that possess olfactory organs from which the vertebrate olfactory organ could possibly have been

[1] 'Ursprung der Wirbelthiere.' Leipzig, 1875, p. 23.

derived by inheritance. Hence it follows either that vertebrates must have acquired or developed an olfactory organ completely *de novo*, or else that their olfactory organ has been formed by gradual modification of some pre-existing structure with accompanying change of function[1]. The first of these alternatives may, I think, be at once dismissed as untenable, and then we are left with the second alternative.

I do not propose to enter here into a detailed discussion of the physiology of smell, but will only remark that what little we do appear to know definitely about it is quite in accordance with the view that smelling is only a modified form of breathing, and that no very violent physiological change would be necessary to convert a gill into an olfactory organ. On the other hand, the sense of smell is something of a totally different nature to sight or hearing; the essence of these latter consists in the appreciation of the relative wave lengths of undulations conveyed by air or ether; while smell appears to be due to direct chemical action on the nerve-endings, requiring the presence of free oxygen (Graham).

In the first part of this paper I have attempted to show that the cranial nerves afford very definite evidence as to the segmentation of the anterior part of the vertebrate head—evidence, indeed, quite as definite as that which they have long been recognised as affording concerning the hinder part of the head. The second part of the paper has shown that the visceral clefts afford equally definite evidence on the same point. In a former paper[2] I have called attention to the fact that the early stages of the brain also afford evidence on this point.

It is a matter of considerable interest that the evidence yielded by these three types of structures respectively, as to the number and situation of the cephalic segments, is identical.

The brain consists in an early stage of a series of vesicular dilatations separated by slight constrictions; of these vesicles the most anterior is the forebrain, and the next the midbrain; while the succeeding vesicles, which form a series decreasing in size from before backwards, and of which the first two at any rate appear to possess considerable constancy, are spoken of collectively as forming the hindbrain.

From each of these brain-vesicles a segmental nerve arises: the forebrain gives origin to the olfactory nerve; the midbrain to the third or oculomotor nerve;[3] from the

[1] Cf. Dohrn, op. cit., "Princip des Functionswechsels."

[2] 'Journal of Anatomy and Physiology.' vol. xl, p. 510.

[3] For a full discussion of the reasons which have led me to consider the

anterior vesicle of the hind brain the fifth or trigeminal nerve arises, and the second hindbrain-vesicle appears to give origin fairly constantly to the seventh or facial nerve; behind this I have not observed any definite relation between the cranial nerves and the brain-vesicles, which latter become very small and of doubtful constancy as to number and relations. This is, however, a matter of little moment, as the evidence afforded by the cranial nerves themselves and by the visceral clefts in the post-auditory part of the head is of an unimpeachable character.

As to the clefts, the most anterior is the olfactory cleft; *vide* figs. 3, 4, 5, and 6. Next to that is the cleft which, following Prof. Parker, I have spoken of as the lachrymal, *i.e.* the cleft in front of the maxillary arch: the relations of the third nerve to this cleft are well shown in fig. 6; it only remains to be added that, of the two branches into which the third nerve divides beyond the distal ganglionic swelling shown in fig. 6, one lies at first behind this cleft, the other in front of it.

We next come to the buccal or mouth cleft, between the maxillary and mandibular arches; the relations of the fifth nerve to this cleft are well known. Behind this is the hyomandibular or spiracular cleft, supplied by the facial nerve; and then the branchial clefts, supplied by the glossopharyngeal and by the several branches of the vagus.

These relations are exhibited more clearly in the following table. In the first column are the numbers of the segments, of which, if we count seven branchial clefts, the full vertebrate number, there are eleven in all; two of these being præoral, and eight postoral. The second column contains the brain vesicles, the third the segmental nerves, and the fourth the corresponding visceral clefts.

third nerve as a segmental nerve, and the fourth and sixth nerves as having no claim to segmental value, *vide* 'Quart. Journ. Micros. Sci.,' Jan., 1878, pp. 23—28, and pp. 32—33. The observations there recorded for the chick I have since verified in the dogfish.

Head Segments of Vertebrates.

Segment.	*Brain-vesicle.*	*Nerve.*	*Cleft.*
Præoral 1	Forebrain	I. Olfactory	Olfactory.
„ 2	Midbrain	III. Oculomotor	Lachrymal.
Oral 3	Hindbrain, 1st vesicle.	V. Trigeminal	Buccal.
Postoral 4	„ 2nd „	VII. Facial	Spiracular or hyomandibular.
„ 5	Hindbrain	IX. Glosso-pharyngeal	1st branchial.
„ 6	„	X. Vagus, 1st branch	2nd „
„ 7	„	„ 2nd „	3rd „
„ 8	„	„ 3rd „	4th „
„ 9	„	„ 4th „	5th „
„ 10	„	„ 5th „	6th „
„ 11	„	„ 6th „	7th „

This table, which has been modelled after the one given by Balfour,[1] differs from this latter in some important points. The differences are most marked in the anterior part of the head, where I have added an olfactory segment, and have attempted to define more accurately the constituents of the second segment by removing the fourth and sixth nerves, and assigning, for reasons discussed elsewhere, the third nerve as the true segmental nerve. At the hinder end of the head I have added two segments for the two hinder branchial clefts of Notidanus and the Marsipobranchii, so that the table is intended to include the full number of head segments of which we have any definite indication in any vertebrate, excepting Amphioxus; though it is by no means intended to exclude the possibility of additional segments having existed at the hinder end of the head in former vertebrates, or actually existing in some living forms.

It will further be noticed that I have placed the visceral clefts, and not the visceral arches, as indicating segments; this is a point of some importance, but one which I do not think we are yet in a position to decide with certainty. The question is, whether the visceral clefts are to be viewed as *intersegmental, i. e.* as corresponding in position to the lines of separation of the original segments by the fusion of which we suppose the vertebrate head to have been formed; or whether they should be considered as *intrasegmental*, as apertures formed in the substance of the segments; in other

[1] Op. cit., p. 216.

words, whether the visceral clefts are formed between successive segments, or through the middle of the segments.

Though the former of these views is usually assumed to be the true one, yet there are, I think, considerations of some weight in favour of the opposite view. In the first place, we must bear in mind that the original proto-vertebral segmentation does not extend to the head, and that the secondary, visceral cleft segmentation appears late, and differs totally from the segmentation of the body, inasmuch as, instead of starting on the dorsal side in the mesoblastic tissue on either side of the neural axis, it arises in, and is limited to, the lateral and ventral walls of the alimentary canal. Instead of arising primarily in the mesoblast, it is a segmentation in which the mesoblast takes no share whatever, except a purely passive one; it is a segmentation produced by the growth of diverticula from the alimentary canal, which come in contact with, and fuse with the external epiblast, and, finally, by perforation of this latter open on to the exterior. Now, it is more in accordance with what we know of the occurrence of lateral diverticula of the alimentary canal in Invertebrata, that these should be segmental rather than intersegmental.

Again, while each cranial segmental nerve supplies two visceral arches, it only supplies one cleft; and, from the analogy of Invertebrata, we should expect that the distribution of each nerve would be to its own segment; while it certainly would be a very remarkable fact that each segmental nerve should supply adjacent halves of two segments.

The distribution of the branchial arteries may also be cited as additional evidence in the same direction; the corresponding vessels in Invertebrata do not occupy the middle of each segment, but follow the intersegmental septa, which septa, according to the view here advocated, would occupy the centres of the vertebrate visceral arches, and so correspond in position with the branchial arteries. On the same view the skeletal elements of the visceral arches would also correspond in position to the intersegmental septa, from which, indeed, they may conceivably have been derived.

This view acquires some additional interest in connection with Dr. Dohrn's suggestion that the visceral clefts are homologues of segmental organs.[1]

The theory above propounded as to the morphology of the vertebrate head, will, I venture to think, throw some light on the nature of the skeletal elements of the head. I will

[1] Op. cit., pp. 10, 11.

here only notice briefly one or two points of importance. On the view here put forward the *trabeculæ cranii*, which lie at the base of the brain, run parallel to the longitudinal axis of the head, and at right angles to the segmental structures, such as the third and olfactory nerves and the corresponding clefts, must be regarded as axial structures, and not as arches, whether neural or hæmal.[1]

Again, my investigations appear to leave no room for doubt that the maxillary arch, the rudiment of the upper jaw, is as fully entitled to rank as a distinct visceral arch as the mandibular, hyoid, or branchial arches. Figs. 3—6 appear to me to afford conclusive evidence on this point.

The morphological nature of the labial cartilages has been matter of much dispute; if the determination of the olfactory organ as a gill cleft be accepted, those at least of the labial cartilages which are grouped round the external aperture of the olfactory organ, and very possibly those also in connection with the gape of the mouth, would appear to be homologues of the extra-branchial cartilages, a suggestion in which I find I have been anticipated by Professor Parker.[2]

I cannot refrain here from referring to the remarkable manner in which the views here put forward agree with the results arrived at by Professor Parker, and embodied in his latest paper.[3] He there expresses himself "satisfied that, in spite of the doubling up of the basis cranii, at the time of its greatest flexure, there are rudiments of three præoral arches, related to *two præoral clefts, the lachrymal and the nasal.*" "Thus we get four pre-auditory, and eight post-auditory clefts, with their nerves; if we add the twelfth (hypoglossal), of the 'Amniota,' we have obtained signs and proofs of thirteen cranial (segmental) nerves, all of these, except the last, forking over visceral clefts, and *hedged in all but the last by visceral bars. The first of the bars is in front of the first or nasal cleft*, the last, or thirteenth, is the hinder bar of the lamprey's branchial basket work." The italics in the above quotation are mine. Though I see no reason for regarding the hypoglossal as a segmental cranial nerve, this extract from Professor Parker's work shows that the study of the skeletal elements of the head

[1] Cf. Parker, "On the Development of the Skull and its Nerves in the Green Turtle," 'Proc. Royal Soc.,' 1879.

[2] 'Trans. Zool. Soc.,' 1876, "On the Structure and Development of the Skull in Sharks and Skates," pp. 212 and 224.

[3] "On the Development of the Skull and its Nerves in the Green Turtle." 'Proc. Royal Soc.' 1879. This was read before the Royal Society on the same evening as the abstract of the present paper.

leads to results almost identical with those at which I have arrived, and affords perhaps the strongest possible confirmation of these results.

Though in the above enumeration of the segmental cranial nerves I have left out the optic nerve, for reasons stated elsewhere,[1] it is quite possible that this nerve may ultimately prove to be of segmental value; in which case it would indicate the existence of a cleft between the olfactory and lachrymal cleft. However, I have as yet completely failed to find any evidence of its segmental nature, and must, for the present, regard it as of a totally different nature to any of the other nerves. The case of the auditory nerve is very different, for there can be little doubt that this is to be viewed as merely a specialised branch of the facial.[2]

If the olfactory organs are really a pair of gill slits, then they must have originally communicated with the mouth cavity; and it becomes a matter of considerable interest to determine whether any traces of such a communication still exist. It is quite possible that the grooves which connect the nasal sacs with the angles of the mouth in the skate and other Elasmobranchs, and which form the rudiments of the posterior narial passages of higher vertebrates, are remnants of this communication. It is difficult to understand what function these grooves subserve in Elasmobranchs, and their apparently irregular presence or absence in closely allied genera would well accord with their being disappearing rudiments. In connection with this point some observations I have recently made on trout and salmon embryos, though incomplete, appear to possess some interest.

Fig. 31 is a transverse section through the anterior part of the head of a salmon embryo just about the time of hatching: the section passes through the anterior borders of the olfactory pits (*olf.*), through the cartilaginous plate formed by the fusion of the two trabeculæ (*tr.*), and, on the ventral side, through a large flattened cavity (*al'.*); this cavity is found, by a study of the sections in front of and behind the one figured, to be an anterior prolongation of the buccal cavity, extending forwards in front of the mouth, underlying the olfactory sacs, and reaching almost to the extreme anterior end of the head.

Fig. 33, which has been already described, is a section taken through the head of an embryo of about the same age as that in fig. 31, but a little further back; it shows this same cavity, which, however, is now not completely closed

[1] 'Quart. Journ. Micros. Sci.,' January, 1878, pp. 23—27.

[2] Balfour, op. cit., p. 213, and self, loc. cit., pp. 34—36.

in the median ventral line, the section passing through the anterior part of the oral aperture.

In figs. 34 and 35 the same structure is shown in longitudinal and vertical section; fig. 35, which is the more superficial of the two, shows the pharynx (*al'.*), with the branchial arches and the anterior continuation of the buccal cavity (*al'.*) Fig. 34, which passes through the root of origin of the olfactory nerve, and therefore, as is evident from fig. 33, very close to the median line, passes also through the mouth; it shows very clearly the manner in which this anterior prolongation (*al'*) extends forwards in front of the anterior margin of the mouth.

I have unfortunately not yet succeeded in tracing the development of this prolongation, and do not even know for certain whether it appears before or after the formation of the mouth, or whether it is lined by hypoblast or epiblast.

At a stage a little later than that just described, when the growth of the anterior part of the head has carried the nose considerably further forwards, this prolongation exists in the form of a pair of cœcal diverticula, stretching forwards from the anterior part of the buccal cavity towards the olfactory pits. These are well shown in fig. 32, a transverse section through the anterior part of the head of a salmon embryo about a week after hatching. The section passes through the extreme anterior end of the forebrain (*f. b.*) in front of the origin of the olfactory nerves, through the two eyes (*o. c.*), the superior recti muscles (*r. s.*), the trabecular plate (*tr.*), the hinder end of the two olfactory pits (*olf.*), and the diverticula of the buccal cavity (*al'.*) close to their anterior terminations. At a stage a little later still, these diverticula appear to shrink and disappear; at least I have failed to recognize them in sections.

Whatever these diverticula may prove to be, their existence is certainly of some interest in connection with the visceral-cleft theory of the olfactory organ; they show, at any rate, that there do exist diverticula of the alimentary canal towards the olfactory organs; they may possibly be taken as indications of a former extension forwards of the alimentary canal to the anterior end of the head; while their paired condition, shown in fig. 32, may perhaps be an indication of relationship to the paired lateral diverticula of the alimentary canal, which form the rudiments of the hinder visceral clefts.

Again, if the olfactory organs are gill clefts and the Schneiderian folds gills, not only must these clefts have originally communicated with the buccal cavity, but the vertebrate

mouth must originally have been in front of them. According to Dr. Dohrn the present vertebrate mouth is formed by the median coalescence of a pair of gill slits; my own investigations lead me to the conclusion that, though these gill slits do contribute to the formation of the mouth, there is in addition a median involution of the epiblast of the under surface of the head, as described by Balfour[1] and others, so that the mouth consists of three elements, a median epiblastic involution and a pair of gill slits. I am inclined also to believe that the fact of the olfactory organs appearing in front of the mouth is due to two causes; firstly, the hypertrophy of the forepart of the head carrying the olfactory sacs forwards; and, secondly, an actual shifting backwards of the median element of the mouth, of which I think there is a certain amount of independent evidence. The anterior end of the notochord is, as is well known, bent completely round on itself, through an angle of fully 180°, *i. e.* as Balfour has already noticed, to a much greater extent than cranial flexure alone will account for. Now, assuming that the notochord is a hypoblastic structure, and that its anterior end remains for a time in connection with the hypoblast, a shrinking back of the hypoblast of the anterior end of the foregut would at once account for this condition of the notochord, and would at the same time cause a displacement backwards of the mouth. It would appear therefore quite possible that the median element of the present vertebrate mouth is the original vertebrate mouth which has undergone a slight displacement backwards, and so has become severed from the olfactory organs.

Perhaps the most serious objection to the visceral-cleft theory of the olfactory organ that is likely to occur at first sight, is the fact that these organs are involutions of the external epiblast, while the visceral clefts are formed by diverticula of the hypoblast of the foregut. While fully admitting the force of this objection, I venture to think that the arguments I have brought forward—the evidence in favour of the segmental value of the olfactory nerve, the close relation, both anatomical and histological, between the olfactory organ and the visceral clefts, the fact that these relations are much more marked in the more primitive than in the more specialised vertebrates, the various identities in time of appearance and in histological structure, and the concurrent testimony of the various incidental circumstances to which I have alluded—are sufficient to outweigh this objection. Moreover, we must bear in mind that slight ingrowths

[1] Op. cit., p. 189.

of the external epiblast towards the hypoblastic outgrowths of the pharynx may occur, and that it is still a matter of uncertainty whether some of the gills are not epiblastic rather than hypoblastic;[1] while, if the diverticula of the alimentary canal described above in the trout and salmon should prove to be hypoblastic, the principal differences between the olfactory organs and the gill clefts would be the gradual shrinking of the most anterior pair of diverticula of the buccal cavity, the ultimate failure on their part to reach the surface, and a corresponding exaggeration of the epiblastic surface involutions, which changes can readily be conceived as following on, and caused by, a slight displacement backwards of the mouth. Since the functional activity of the gills as such depends on the constant passage of a stream of water through the mouth into the buccal cavity and then out through the gill slits, it follows that if the mouth were changed in position so as to be situated behind instead of in front of, the first pair of gills, the function of these gills would be materially interfered with, while their position at the anterior extremity of the head and their consequent potential utility, would favour their preservation in a modified form, and with modified function.

On the Brain *of the* Cockroach, Blatta orientalis. By E. T. Newton, F.G.S., H. M. Geological Survey. With Plates XV and XVI.

The common cockroach, *Blatta orientalis*, has been found a very convenient insect to take as a type of its order, both on account of its generalised structure, and the readiness with which it may be obtained, in any numbers, at all seasons of the year; consequently it has been dissected largely in our biological schools.

It seemed desirable, therefore, when the structure of the brain of certain insects was being investigated by several continental naturalists, that we should make ourselves somewhat better acquainted with the brain of our typical insect the cockroach, for this had not been worked out as carefully as it merited. And further, inasmuch as in certain particulars this insect is less specialised than some of those, the brains of which have been examined, it seemed

[1] Balfour, op. cit., pp. 210, 211.

probable that we should here find the brain in a less specialised condition. The facts which have now been made out show that, in the structure of its brain, the cockroach holds a median position; possessing as it does all the structures (excepting the ocelli nerves, unless, indeed, the white spots near the bases of the antennæ should prove to be rudimentary ocelli) which have been described in other insects; but at the same time certain of these parts are not quite so complicated and are, therefore, more easily understood.

It was not until I had nearly finished my own investigations, and was about to publish the results, that I saw the memoir by Dr. Flögel ('Zeitsch. wissen. Zool.,' 1878, vol. xxx, supple., p. 556), in which the internal structure of the brain of *Blatta* is very fully described. On the whole the results which I had obtained agreed with those of Dr. Flögel; but as my paper did not cover the same ground, and, moreover, as little or nothing had appeared in British journals on the minute structure of insects' brains, it still seemed desirable to publish the results of my own work. And, further, as the Blatta's brain seems likely to be taken as the type for comparison in future investigations, it is the more necessary to have it fully illustrated, and the photograph of one section only, which is all that is given by Flögel of the Blatta brain, seemed to me quite inadequate for its proper comprehension. Even with a series of sections and drawings before me, it was by no means easy to get a clear conception of the forms of some of the internal parts, and I therefore constructed a model from a series of sections (*vide* 'Quekett Journal,' 1879, vol. v, p. 150), which gave me a far better knowledge of these parts than I had found it possible to get in any other way.

The complicated internal structure of the brain of insects, appears to have been first pointed out by M. Dujardin, and attention is more especially directed to this, because the correctness and clearness of his descriptions do not appear to me to have been sufficiently appreciated.

M. Dujardin, in 1850 ('Ann. d. Sci. Nat.,' t. xiv, p. 195), pointed out that in some insects there were to be seen upon the upper part of the brain certain convoluted portions which he compared to the convolutions of the mammalian brain, and, inasmuch as they seemed to be more developed in those insects which are remarkable for their intelligence, such as ants, bees, wasps, &c., he seemed to think the intelligence of insects stood in direct relationship to the development of these bodies.

The form of these structures is described by the same author as being, when fully developed, as in the bee, like a pair of discs upon each side, each disc being folded together and bent downwards before and behind, its border being thickened and the inner portion radiated. By very careful dissection he found these bodies to be connected on each side with a short pedicle, which bifurcates below to end in two tubercles. One of these tubercles is directed towards the middle line and approaches, but does not touch, the corresponding process of the opposite side. The second tubercle is directed forwards and is in close relation to the front wall of the head, being only covered by the pia mater. These convoluted bodies and the stalks upon which they are mounted are compared by Dujardin to certain kinds of mushrooms, and this idea has been retained by more recent writers on the subject.

The physiological experiments of Faivre in 1857 ('Ann. d. Sci. Nat.,' t. viii, p. 245) upon the brain of *Dytiscus* in relation to locomotion, are of very considerable interest, showing, as they appear to do, that the power of co-ordinating the movements of the body is lodged in the infra-œsophageal ganglia. And such being the case, both the upper and lower pairs of ganglia ought to be regarded as forming parts of the insect's brain.

Dr. Franz Leydig, in 1864 ('Vom Bau des thierischen Körpers,' &c.), entered fully into the structure of the nervous system of insects, and described the histology of the various parts of the brain. The method of preparation which he adopted was to preserve the insect in absolute alcohol, then to remove the brain, and render it transparent with dilute potash solution, or glycerine. As regards the general structure of the so-called mushroom body and its stem, Leydig makes little advance upon what was done by Dujardin, but, in consequence of his method of preparation, as it seems, was misled into describing as a giant nucleus upon each side of the middle of the brain, the peculiar mass of nervous matter, which Dujardin had correctly described as a process extending forwards to the front surface of the brain.

In 1875 Dr. Rabl Rückhard ('Archiv. f. Anat. u. Phys.,' p. 480), described the structure of the brain of the black ant (*Camponotus ligniperdus*), adopting chiefly the method of preparation made use of by Leydig. He was enabled to make out the head of the mushroom body with its stalk; he also saw the appearance described by Leydig as a giant nucleus, but believed it to be the optical section of cylindri-

cal commissures passing from the front to the back of the brain. He mentions also that, in the bee, he has been able to dissect out the process which passes to the front of the brain, as described by Dujardin. It is this which, when seen from before, gives the appearance of a central nucleus in each hemisphere. The head of the mushroom body he described as forming a complete ring, which he was able to separate from the surrounding parts. From what we now know of the structure of these mushroom bodies, it is clear that these parts must have been separated from their attachments before they could give the appearance of closed rings. We shall, I think, see presently that Dujardin was much more correct in speaking of them as folded discs.

Dr. Dietl, in 1876 ('Zeitsch. wissen. Zool.,' Band xxvii, p. 488), published an elaborate description of the brains of the bee, mole-cricket, grasshopper, &c. The method employed by this author was, to cut up in definite directions brains which had been hardened in osmic acid. In the main the results of his observations accord with those of Dujardin and Rabl Rückhard. He agrees with them as to the existence in the bee of two mushroom bodies in each hemisphere, mounted upon downwardly-directed stalks, and also as to the cylinder of nervous matter passing forwards to end abruptly upon the front of the brain. He further agrees with Rabl Rüchkard that the giant nucleus of Leydig is the optical section of this nervous cylinder. In the mole-cricket Dietl describes only one mushroom body on each side, and the stem passing downwards from this is said to divide into two parts, one of these ending in the middle line, whilst the other forms the cylinder ending upon the front of the brain. The various histological elements are described in detail, as they are found in the various parts of the brain. Dr. Dietl finds the nervous matter in invertebrate brains under the three following conditions:—1. Ganglionic cells, as they are called, and allied structures, free protoplasmic nuclei. 2 Nerve-fibres of the most different sizes. 3. "*Marksubstanz*," a peculiar arrangement of nervous matter, which appears sometimes as fine fibrillæ, with an axial arrangement, sometimes as a very fine network of different thicknesses, and sometimes as thin lamellæ, or altogether homogeneous. Under all these forms this third group of textures is characterised by turning very dark under the influence of osmic acid, whilst the other elements are only turned brown.

Another valuable addition to our knowledge of insect

brains was made by the publication of the memoir by E. Berger in 1878 ('Arbeiten des Zoolog., Instituts zu Wien.,' Bd. i, Heft ii, p. 173). This memoir is largely occupied with the description of the retina and the structures to be found in the optic lobes of Arthropods. It is extremely interesting to find that the peculiar oval bodies which Leydig figured as occurring in the optic lobe of *Dytiscus* ('Tafeln z. Vergleich,' 1864), and were afterwards described and figured by me as "*lenticular bodies*" in the eye of the lobster ('Quart. Jour. Micro. Sci.,' 1873, vol. xiii, p. 336), are to be found in a more or less modified form in all the insects and crustacea described by E. Berger. The remarkable crossing of the nerve-fibres between the retina and the lenticular bodies is seen not to be peculiar to the lobster. The kidney-shaped body, which is such a distinct part in the lobster's optic ganglion, appears to be represented in the Squilla by the body marked G in Berger's figure 32. The brains of a number of insects are described, including examples from the *Neuroptera*, *Coleoptera*, *Diptera*, *Lepidoptera*, *Hymenoptera*, and *Orthoptera*, and in each of these the author seems to have found the homologues of the mushroom bodies, although in some—the Diptera, for example—they are very rudimentary. Not a little important are the facts recorded relative to the transverse commissures of the brain. It seems to me somewhat doubtful whether the paired structures which have been shown by several authors to be present in the brains of Crustacea, are really the homologues of the mushroom bodies of the insect's brain. Dietl has shown ('Sitz. Kaiser. Akad. d. Wissen.,' 1878, Band 77, p. 584) that in the crayfish these bodies are connected with the optic nerve, and he calls them optic lobes. Among the Insecta this connection, if it exists, has yet to be demonstrated.

Dr. Flögel, in his paper already referred to (loc. cit.), takes the Blatta brain as a typical form, and describes its internal structure. Great stress is laid upon the persistent presence in all orders of insects of that peculiar median laminated structure, described by Dietl, which is now called by Flögel the central body "*Centralkörper*." In Blatta there is a pair of mushroom bodies in each hemisphere. The cylinder of fibres passing to the front of the brain is very large, and is termed the anterior horn "*Vorderhorn*." The description of the minute elements agrees with Dietl's observations mentioned above. In the latter part of this paper the brains of various insects are described, which have been taken from the different orders, and a tabular scheme is given of

the relations of these orders, based chiefly upon the degree of development of the mushroom bodies.

Blatta (*Periplaneta*) *orientalis*.

General form of the brain.—When the chitinous covering of the upper and front part of a cockroach's head is removed, together with the tissues which lie just within it, the brain, or supra-œsophageal ganglion, is displayed as a pearly white body, occupying but a small portion of the cavity of the head (fig. 1). In this view the brain is seen to consist of two rounded masses above, separated from each other by a deep median fissure. From the outer sides of these hemispheres, as they might be termed, the large nerves are given off to the eyes (*op.*). Below are two smaller rounded masses, marked off from the upper ones by a depression, these are the antennary lobes (*anl.*), from the outer side of each of these a nerve passes off to one of the antennæ. A side view of the head dissected so as to expose the brain (fig. 2) shows the latter to be placed very near the front wall, while the space behind it is occupied to a large extent by the muscles of the jaws.

At first sight the only nerves given off from this upper division of the brain seem to be the optic and antennary nerves, but I have now been able to trace four other pairs; these, however, are very small.

(1.) On more than one occasion, when opening the head of a cockroach, I have observed a very delicate white fibre passing from the front surface of the brain towards the front wall of the head; but thinking it was merely a tracheal vessel, I had not troubled to trace its distribution. After seeing Dr. Flögel's statement that a nerve passes out from the front of the brain on each side, in the region where I had noticed this white fibre, I searched again, and now had the satisfaction not only of finding the nerves in the position indicated (fig. 1 *nws*), but also of tracing them most clearly to those peculiar oval, silvery patches, which are situated on the front of the head, just above and within the antennæ (*ws.*). It appeared to me that one of these nerves, before reaching the silvery patch, gave off a branch which passed round to the side of the brain, just above the optic nerve; but I could not trace it upon the opposite side, and I failed altogether to see it in another specimen.

(2.) Another nerve is to be found passing off from just underneath the antennary lobe on each side (figs. 1 and 2 *anm.*), and these I have been able to trace to the muscles of

the antennæ, which lie within the head just below the base of the antennæ.

(3.) Upon each side of the brain, a little behind the antennary nerve, a third very small nerve may be found (fig. 2 *n*), the distribution of which I have not yet traced.

(4.) The stomato-gastric ganglia join the brain at its back part (fig. 4 *a. stg.*).

From the lower and back part of the brain on each side, the large pair of commissures (fig. 2 *o. com.*) pass downwards and backwards to the infra-œsophageal ganglia (*inf. g.*). From the front of each commissure a broad band of fibres arises, which passes forwards for a short distance upon the sides of the œsophagus, and then divides into two branches; one of these curves forwards and upwards to meet with its fellow of the opposite side in the frontal ganglion (fig. 2 *f g.*). The second branch appears hitherto to have escaped notice, it passes forwards and downwards (fig. 2 *ln.*), and the two may be traced into the labrum, as far as the round white spots, which are situated, one on each side, upon the inner surface of that appendage.

The infra-œsophageal ganglia are situated quite close to the back part of the head, being only separated from the submentum by a thin band of muscles. The nerves arising from these ganglia are shown in figures 2 and 3. The majority of them were most easily traced when approached from the back. For this purpose, the head was fixed in wax with the front surface downwards, the submentum removed, and then the parts below gradually displayed. Fig. 3 is the result of careful dissections of numerous individuals. If the commissures passing into the head from the body ganglia be traced forwards, it will be found that, just within the foramen magnum, where they join the infra-œsophageal ganglia, a minute nerve is given off on each side (figs. 2 and 3 *nf.*), which appears to be distributed to the muscles in the immediate vicinity of the foramen. In one instance there seemed to be two or three of these minute fibres. With the exception of the nerves just mentioned, no fibres were to be found passing off from the hinder surface of these ganglia; at the lowermost angles the pair of nerves (*lm.*) pass off, one to each side of the labium; each of these nerves at length divides into two, sending a branch into the inner and outer divisions of the labium. Immediately in front of each labial nerve, or perhaps arising from it, there is another very minute one, which passes outwards and is lost in the surrounding muscles. A little further forwards, on side, a nerve is given off to the maxilla (*mx.*). From

the base of this, and close to the ganglion itself, a minute nerve is given off, which, passing directly outwards, could be traced to the proximal part of the stipes. Further down the maxillary nerve divides into two, and then the outer division into two again, thus forming three branches, which no doubt supply the three distal divisions of the maxilla. From the front and lower part of the ganglia, two large nerves pass downwards and forwards, close together for some little distance, and then diverging, each passes into the mandible of its own side. At the base of this nerve again, a minute fibre arises, as in the case of the nerves of the maxilla and labium, and this was found to pass into the mandible at its most proximal part. Although the distribution of the fine fibre accompanying the labial nerve could not be traced, it seems probable that it supplies the basal portion of the labium; and if such should prove to be the case, then each of the mouth appendages will be seen to be supplied with two nerves, a larger and a smaller one.

At present I have been unable to trace any nerves or nerve into the lingua.

The stomato-gastric nerves, as stated above, arise by two roots, one from each œsophageal commissure, which unite in the frontal ganglion. The single *nervus recurrens* (fig. 4 *f n*), passing back from the frontal ganglion (figs. 1 and 2 *f g.*), runs along the œsophagus under the brain, and is connected with the stomato-gastric ganglia, situated at the back of the brain. The most successful dissection of these ganglia which I have been able to make is represented in fig. 4, but this has been verified by several other preparations. It will be seen that the *nervus recurrens* becomes much thickened at the point where it joins, on each side, a short stem connected with the hinder end of an elongated, somewhat spindle-shaped, ganglion. Each of these ganglia is connected posteriorly with a second oval ganglion, and anteriorly a short bundle of fibres connects it with the back part of the brain. In one or two dissections I could trace these nerves some little way under the back of the brain, but failed to convince myself as to whether they joined the brain or not; however, in another dissection of a very large cockroach, these nerves could be seen joining the back of the brain well underneath, but no nerve could be traced passing forward from this point. Nervous filaments are given off from the posterior pair of ganglia; and in another preparation fibres were seen to be given off from the anterior pair also.

In the *Sphynx* moth, according to Newport ('Phil. Trans.,'

1834), these stomato-gastric ganglia are connected with the brain; and Leydig states that the same thing occurs in *Dytiscus*. Flögel states, on the authority of Kupffer, that this connection is also found in *Blatta*; and, on the same authority, they are said to send fibres to the salivary glands.

Internal Structure of the Brain.

The internal structures of the brain, which are described in the following pages, have been worked out chiefly by means of series of sections, cut in definite directions, but this has to some extent been supplemented by dissections. Brains hardened in osmic acid, after the manner adopted by Dietl, were found to be most satisfactory, but others hardened in alcohol and stained with carmine were very useful for comparison. The most instructive sections were those which have been called "frontal sections;" that is, cut as nearly as possible parallel with the front surface of the brain; the first section including portions of both the hemispheres and the antennary lobes. One brain, which had been hardened in osmic acid, was cut in this way into thirty-four sections, each about the $\frac{1}{1000}$th of an inch in thickness, and from these I was enabled to construct the model already alluded to. From this series of section those have been selected for illustration which it was thought would best explain the various structures, and will be found represented on Plate XVI.

Some of the internal parts of the insects' brain have received different names from different authors, and hence several names have in some cases been given to one and the same part. Dr. Flögel, evidently seeing the difficulty likely to arise from this loose nomenclature, has suggested certain terms which might be used by future writers on the subject. Most of these terms would, no doubt, have been at once adopted; but, unfortunately, they are given in German, and it would be necessary for other than German writers to render them in equivalent terms of their own language. I would suggest, therefore, that we now, once for all, latinise these terms, and thus obviate this difficulty also. The mass of nervous matter found at the lower part in each hemisphere (marked *t* in the accompanying figures), and called by Flögel the "*Balken*," may be called the *trabecula*. That peculiar mass of nervous tissue passing off from the *trabecula*, and ending abruptly on the front of the brain, termed by the same author "*Vorderhorn*," would then become the *anterior cornu*; but this name

cannot be adopted, as it is already in use for a region in the human brain, and would certainly lead to much confusion. I propose, therefore, to name this part the *cauliculus* (*cau* in figures). It will be convenient to call the hinder branch given off from the *trabecula* (that is, the "*Hinterast*" of Flögel, and the "*Pilzstiel*" of Dietl) the *peduncle* (*p.* in figures) in allusion to its being the support of the so-called mushroom body. It seems to me undesirable that this latter name should be altogether abandoned, seeing that it has been much used, and I propose, therefore, that each of these structures, taken as a whole, be known as a *corpus fungiforme*, while the inner trough-like portion of it, called by Flögel the "*Becher*," will become the *calix*; as there are two of these on each side, they will be distinguished by the prefix *inner* or *outer* (*icx.*, *ocx.*, in figures). And the calicular cells may then be distinguished according to the portion they occupy in the *calix*. The "*Centralkörper*" will become the *corpus centrale*. I should prefer to retain the name of *antennary lobe* for that part from which the antennary nerve passes off, until we are more perfectly acquainted with the functions of the antennæ.

It is proposed, in the first place, to describe in a general way the series of sections, and afterwards to consider each part separately.

The first section consists very largely of the cortical cells of the hemispheres, but includes a portion of one of the antennary lobes. At the upper part on each side is the rounded end of the *cauliculus*. In section No. 2 (fig. 5), the *cauliculus*, which is strongly curved, occupies a large portion of each hemisphere; it is sharply defined from the surrounding parts, more especially from the mass of cells arching over it above, which are coloured yellow by the osmic acid. Fibres, arising from the middle line of the brain, are seen passing outwards and crossing the lower part of the *cauliculus*.

In section No. 3 the first traces of the *calices* of the *corpora fungiformia* are seen as elongated patches above the *cauliculus*, and within the cellular cap. In section No. 4 the *calices* have increased in size. In section No. 5 the *trabeculæ* are seen for the first time, passing on each side from the lower end of the *cauliculus* downwards to the middle line. In section 6 (fig. 6) we have the first indication of the *peduncle*.

In the following sections these processes increase in size, while the *cauliculi* decrease; the *calices* also increase and become more and more deeply curved (fig. 7), until in

section 13 (fig. 8) the *peduncles* have reached and joined the outer calix on each side, the *cauliculus* having almost disappeared. In section 14 the *peduncles* have joined the inner *calices* also, and this connection is seen in each section as far as the 19th, the *calices* at the same time exhibiting their deepest curvature. In section 20 (fig. 9) the *peduncle* on each side has entirely disappeared, the *trabecula* alone being seen in the middle line below. In the succeeding sections the *trabeculæ* become gradually less, but can be traced as far as the 28th section. Passing back from the 18th or 19th section, the *calices* get less curved and smaller, and traces of them are last seen in the 25th section. The commissures to the infra-œsophageal ganglia are reached in the 18th section, and become larger and larger through the remainder of the series.

The Trabeculæ with their Cauliculi and Peduncles.—The *trabecula* in each hemisphere commences abruptly in the 5th section, and is seen extending from the middle line below (where it abuts upon, but apparently does not join, its fellow of the opposite side) obliquely upwards and outwards to join the lower part of the *cauliculus* (fig. 6). Passing backwards the *trabecula* continues about the same size until it has received the *peduncle*, behind which point it gradually decreases (fig. 9), and is altogether lost before the back of the brain is reached (see figs. 15 and 17).

Each *cauliculus* is a large mass of nervous matter, continuous with the outer part of the *trabecula*, the junction extending as far back as the hinder part of the *peduncle* (fig. 15). Seen from the front it curves upwards and outwards, presenting a convex surface inwards, and a concavity outwards (figs. 5, 6, and 17). Its thickness from before backwards is greater than it is from side to side, and consequently it presents an oval figure in horizontal sections. The upper portion is truncated by being closely applied to the under surface of the outer *calix*, while the inner convex surface is closely overlaid by the inner *calix*. The line of demarcation between the *calices* and the *cauliculus* is very distinct, and there seems to be no nervous connection between them. Above and in front this *cauliculus* extends to the front surface of the hemisphere, where it appears to be merely covered by the thin investing membrane of the brain.

The *peduncle*, or stem of the *corpora fungiformia*, arises from the *trabecula* by a wide base extending from the 6th to the 20th section. Its upper part is very much smaller than the *cauliculus*. In a front view the *peduncle* is seen to continue upwards the curve of the trabecula, and to present

a convex surface outwards (figs. 8 and 17). Quite towards its upper end the *peduncle* divides into two parts, one of which joins the outer (fig. 13), and the other the inner *calix*.

With regard to the histology of these structures I am now able to give the following particulars:—The upper part of the *peduncles*, where they join the *calices*, shows a most definite fibrous structure even with a low power of the microscope, and this is seen extending downwards more or less distinctly as far as their junction with the *trabeculæ*. The *trabeculæ* themselves and the *cauliculi* present only a finely granular or dotted appearance unless examined with a high power. Under a $\frac{1}{10}$ immersion both these parts exhibit a fine reticulation, the meshes of which have, perhaps, a diameter of $\frac{1}{10000}$ of an inch, but they are extremely difficult to define. The *peduncles*, with the same amplification, show a similar network, but not quite so fine, and the meshes are more elongated (fig. 14), especially towards the upper part, and it is this which gives it a fibrous appearance. It is, in fact, a bundle of fibres which freely anastomose with each other. The peculiar system of bent lines, mentioned by Flögel, is to be seen in horizontal or oblique sections, where the *cauliculi* join the *trabeculæ*, and in frontal sections where the latter join the *peduncles* (figs. 7, 8 *p*.).

The manner in which these remarkable nervous structures are connected with the other parts of the brain and nervous system have yet to be established. The only parts at present known to be connected with them are the *corpora fungiformia*. The nervous fibres which surround them on all sides seem to be merely in close apposition, and not to be really united with them. Towards the back of the brain, where the *trabeculæ* become reduced in size, they also become less and less clearly separated from the surrounding parts, and it seems possible that there is some connection in this region. Possibly some of the fibres which extend downwards from the large cortical ganglionic cells at the back of the brain (fig. 10) join the *trabeculæ*, but I have been unable to trace any such connection. One would naturally expect that such large and important parts of the brain, as the *trabeculæ* and its appendages, the *cauliculi*, *peduncles*, and *corpora fungiformia*, would be very obviously connected with the rest of the brain, or, at least, that we should find fibres extending from it into the œsophageal commissures.

Corpora fungiformia.—There are two of these bodies in each hemisphere, an inner and an outer one, both extending from near the front almost to the back of the brain. Each

of these consists of a *calix* (figs. 15, 16 *ocx.*, *icx.*), and a cap-like covering of small cells. Each *calix* is, perhaps, best described as having the form of a trough, the sides of which are deepest in the middle and much shallower towards the ends, more especially towards the front. The inner *calix* is rather larger than the outer one, and the two are closely applied to each other and covered by the mass of cells, which forms one cap over the pair of *calices*. The appearance presented by these bodies in frontal sections may be seen in figs. 5 to 10, but the general form will be best understood by reference to figs. 15 to 17, which represent those parts in the model already mentioned. The *peduncles* are connected with the *calices* a little behind their middle region, and where this takes place the *calices* have their greatest depth.

When stained with osmic acid the *calices* become very dark and ordinarily appear in sections to be composed of small dark bodies, which, at first, might be mistaken for cells. Their inner surfaces, more especially near the *peduncles* (fig. 8), are covered with fine fibres, which run in the direction of the peduncles. The small cells which fill the *calices* extend just over their margins both before and behind, as well as at the sides. They are stained a bright yellow by osmic acid, and are regarded by both Dietl and Flögel as being cells in which the protoplasm is so reduced that the nuclei only are visible. However this may be, they certainly seem to me to be of quite a different nature from the cortical ganglionic cells, from which they always seem to be sharply separated. The ganglionic cells, wherever they are clearly shown, are seen to possess not only a nucleus, but also a very definite nucleolus, whilst in the calicular cells I have failed to find any nucleolus, even in those larger ones which occupy the base or deepest part of each *calix*. Very fine dark fibres are seen branching out and penetrating in between these cells, enclosing them, apparently, in a complete network. Passing inwards these fibres collect into larger branches, and these meeting at the walls of the *calix*, form a kind of festoons (fig. 6). In the neighbourhood of the *peduncles* these branches may be seen passing into the fibres of the inner walls which run down into the *peduncles* (figs. 8 and 12). Whether these fibres are wholly composed of nervous matter, or are to some extent accompanied by connective tissue, it is not easy to say.

When extremely thin sections are examined with a high power, the ultimate structure of the calicular walls still remains obscure; but with care one can see that the fibres

forming the inner part of the wall anastomose freely, so as to form a network of broad fibres, with elongated interspaces having the appearance of cells. These fibres are intimately united with a similar, but much finer, network, which makes up the greatest part of the calicular walls. In the latter portion may be seen rounded transparent areas of very different sizes, and other irregular patches of a darker and granular substance.

Corpus centrale.—The peculiar laminated arrrangement of nervous matter, described by Dietl in the bee and mole-cricket as a median commissural system, is called by Flögel the central body. This structure is not so clearly defined in my preparation of the cockroach as it is in the two insects just mentioned. In the series of frontal sections (34) from which this description is taken, the lamination of the central granular substance is first seen in the thirteenth from the front (fig. 8 *c*). Here the granular mass is indistinctly divided into four parts, and is surrounded by irregular cells and interlacing fibres; from the latter fibrous bands are seen passing upwards and outwards, some of which may be traced to the optic nerve. Below the granular mass, the cells are partly divided into groups by dark fibres passing down among them. In the 12th section only a small portion of the granular substance is seen, while the cells and fibres are more abundant and evident. In the 14th section the granular substance is clearly divided into six parts, which occupy nearly the whole width between the *trabeculæ*. Below this the cells are beginning to give place to granular matter, and this shows some indication of being divided into plates (fig. 11). Passing to the 19th and 20th sections, we find that in the upper portion the divisions of the granular mass have increased in number to twelve or fourteen, these divisions, however, are not so clearly marked off as in the more anterior sections. Above this there is a row of very transparent cells, and below there is little else than granular matter and fibres, from among which dark branches pass upwards, and dividing, separate the granular matter into its laminæ. In this region fibres are seen passing off from the sides of the *corpus centrale*, and arching over the now reduced *trabeculæ*, extend in the direction of the œsophageal commissures. The divisions of the granular matter are still to be traced in the 22nd and 23rd sections, and continue to occupy as great a width; notwithstanding this, the granular matter has almost entirely given place to cells in the 24th section. Throughout its length, the upper surface of the

corpus centrale is intimately connected by a network of fibres with the large mass of the ganglionic cells lying above them. But here, again, it is probable that connective tissue combines with the nervous tissue to produce the appearance presented by their sections. When the thinnest sections of the *corpus centrale* are very highly magnified, the fibres from the surrounding cells may be seen collecting together and forming the partitions which give this body its laminated appearance. These partitions seem to be intimately connected with the enclosed granular matter, which itself gives evidence of being made up of a network of fibres; but this was not clearly shown.

With regard to the general form of the *corpus centrale*, if we restrict this term to the laminated granular matter, it will be obvious, from what has been said above, that it has a broad truncated hinder end, and diminishes in size towards the front, the number of the laminæ gradually increasing from before backwards. In frontal sections the upper surface is convex. The form of the lower surface will be best understood by reference to the figures (8, 11, 9). Anteriorly, it passes gradually into the cells lying below, which fill up the space between the trabeculæ. Posteriorly the granular substance occupies the whole of this space, and is, therefore, pointed below. The sides are rounded.

I find that Flögel's description of the central body does not agree with my own observations, as given above; but this, to some extent at least, is due to our sections not being in precisely the same plane, and partly, perhaps, to our not including in the description exactly the same parts. With regard to the number of the laminæ (Flögel mentions eight), my specimens show most clearly an increase in number, from before backwards, as above described.

Optic ganglion.—I have not yet had the opportunity of working out the structure of this complicated apparatus so fully as it deserves, and can only in the present paper give the following brief description. Horizontal sections show two lenticular bodies placed obliquely and surrounded by a thick layer of cells. The nerve fibres passing from the front and back parts of the eye cross before entering the first and smallest lenticular body; they cross again on leaving it, and before entering the second and larger lenticular body. Between the latter and the brain the fibres cross for the third time. After entering the hemispheres some of the fibres may be seen passing forwards into the mass of cells lying in front of the *corpus centrale*; while there are indications of others passing across near the

back of the brain to join similar fibres from the opposite side.

Antennary lobes.—These are large in the cockroach, and in sections present very much the same structure as Dietl has described in the bee. In whatever direction they are cut they present the appearance of being composed of a number of large cell-like bodies, with fibres passing in between them in every direction, the whole being surrounded by a layer of large ganglionic cells. The interior cell-like bodies are found throughout the mass of the antennary lobe in the cockroach, whilst in the bee they are confined to the periphery. When examined more closely the large cell-like bodies are found not to be cells, but to be made up of a delicate network of fibres, as described by Dietl and Flögel. It was only with a high magnifying power ($\frac{1}{18}$ immersion) that this network could be traced, and then it was by no means distinct; the interspaces still appeared granular, with minute translucent spots. The spaces between the rounded bodies are seen to contain cells as well as fibres; indeed, it may be said that the cortical ganglionic cells extend into the interior of the lobe. The fibres anastomose with each other, and are continuous, on the one hand, with the fine network of the rounded bodies, and, on the other, with the antennary and commissural nerve-fibres. The ultimate structure of these rounded bodies is very similar to that of the *calices*, but it is coarser, and many of the transparent spaces are much larger.

From the inner side of the antennary lobe fibres are given off, which pass under the *trabeculæ*, and unite with similar fibres from the opposite side. Posteriorly, this lobe is connected with the œsophageal commissure, and certain fibres may be traced inwards to the cells around the *corpus centrale*.

Just below the antennary lobe, and in the œsophageal commissures, close to the spot where the nerve to the frontal ganglion arises, there is a small rounded body, composed of dots of granular matter, not unlike that of the *calices*. This body seems to be the homologue of a similar structure in the mole-cricket described by Dietl. I have not been able to trace its relations to the surrounding parts.

Cortical ganglionic cells.—The brain is almost surrounded by these large cells, excepting above, in the region occupied by the *corpora fungiformia*, and, probably, they do not extend over the *cauliculi*. These ganglionic nucleated cells vary much in size, some of them being very large, and they

are not stained so bright a yellow by the osmic acid as the cells of the *corpora fungiformia*.

These ganglionic cells are very numerous at the back of the brain (fig. 10), they extend inwards between the *corpora fungiformia* and the so-called primary lobe; they fill the median groove above the *corpus centrale* (figs. 5 to 10); they are found in abundance in the angles and spaces between the antennary lobes and the rest of the brain; and, as already mentioned, they form a thick layer over the optic ganglion.

These cells appear to be surrounded by connective tissue, which also seems to form a large part of the fibrous bands, seen passing off from them, especially at the back part of the brain (fig. 10), but at the same time the granular cell contents may be seen in some instance, extending into the fibres (fig. 13). These fibres at the back of the brain (fig. 10) pass downwards almost vertically to the region of the *trabeculæ* and then turn outwards. The cells of the median sulcus are connected, as we have seen, with the fibres and cells of the *corpus centrale*, and just in front of the *trabeculæ* large fibres pass down in the middle line into a peculiar fan-like arrangement of cells found on the base of the brain in this region.

The MICROPHYTES *which have been found in the* BLOOD *and their* RELATION *to* DISEASE.[1] By TIMOTHY RICHARDS LEWIS, M.B., Surgeon, Army Medical Department; Fellow of the Calcutta University. (With Plate XVII.)

BEFORE entering on a minute description of the microscopic organisms found in the blood which are more allied to plants than to animals, it will be advantageous to consider to what special subdivisions of the vegetable kingdom these bodies seem to belong. No small amount of confusion has arisen from want of a clear knowledge of this point, especially on the part of strictly medical writers who have discussed the subject of the connection of disease with vegetable parasites. Nägeli, in his remarkably suggestive work,[2] recently published, has placed this

[1] Forms Part I of the Memoir on the Microzoa and Microphytes of the Blood, which appears as an Appendix to the 'Fourteenth Annual Report of the Sanitary Commissioners with the Government of India.'—[ED.]

[2] 'Die Niederen Pilze in ihren Beziehungen zu den Infectionskrankheiten und der Gesundheitspflege,' München, 1877.

matter in a very clear light, and, being an authority of the first rank, especially on the botanical phase of the subject which forms the text of this paper, his statements on this particular point are worthy of exceptional attention. The forms of plant-life which have been recognised as having been more or less closely associated with changes in living animal substances are the lower kinds of fungi. These Nägeli separates into three groups: (1) *Moulds*, characterised by branched, segmented, or unsegmented filaments; (2) *Sprouting fungi*, yeast cells of various kinds, consisting of more or less oval corpuscles, which multiply by means of sprouts from their surfaces; and (3) *Cleft-fungi* or *Schizomycetes*—minute spherical or oval bodies, which are multiplied by fission only, and which sometimes remain isolated, at others form unbranched rows (rods, threads, &c.), but only occasionally present a cubiform aspect. To this group the *bacterium, vibrio, vibrio-bacillus, spirillum*, &c., belong.

Nägeli writes: "I have separated the lower forms of fungi into three groups. On account of many practical questions it is of importance to know whether specific differences really exist, or whether we have to do with the same species under different conditions, it being possible that different fungi possessed a 'mould,' a 'sprout,' or a 'cleft' form. This is a subject which has formed the subject of debate during the last sixteen years, and many observations have been recorded for the purpose of showing that, as a result of cultivation experiments, the most opposite forms have been seen to pass from one into the other." With reference to this point Nägeli forcibly points out the fallacies to which men are liable in drawing conclusions from cultivation experiments, and says that, in many respects, it would be as rational for the husbandman to assert that the weeds in his field were the result of transformations which the seed of wheat previously sown had undergone. No one would believe such a statement, for the seeds of weeds are large enough to be easily recognised, whereas the germs of fungi are of microscopic dimensions —those of the *schizomycetes* often barely distinguishable with the highest powers; hence the assertions which have been made regarding the transition of such minute organisms cannot easily be controlled. "Moreover," adds Nägeli, "the rapid and superficial observer has a marked advantage; the conclusions which he has arrived at as the result of a so-called uncontaminated cultivation [*Reinkultur*] of a single week's duration may require years of labour on the part of the thoroughly competent observer to disprove."

This question has of late years been investigated by many distinguished *savants*, notably by Professor de Bary, of Strasburg. He has shown that a fungus undergoes but a very limited and

well-defined range of changes. Nägeli, as the result of his own observations, declares that, of the three groups of fungi above referred to, the "mould" and "sprout" fungi are closely related, but that, with one exception, they have not yet been seen to pass from one form into the other. The exception consists in the circumstance that a certain species of mucor (a mould) has been observed to present the two forms of vegetation—the filamentous and the sprouting. Fission-fungi, however, do not stand in any genetic relation to either of the other two groups, for they neither give rise to other fungal forms nor originate from them; hence it is distinctly laid down that they do not germinate. In this it would appear that Nägeli and de Bary are completely in accord. Nägeli states that it is comparatively easy to demonstrate that the "fission" group of fungi are not transformed into other groups, from the circumstance that members of the latter, when present in a solution, are killed at a lower temperature than those of the former. This peculiarity, however, renders it much more difficult to show that other (the "mould" and "sprout") groups do not give rise to *schizomycetes*, as it is impossible so to isolate the germs of other fungi as to exclude this group. Eventually, however, he was able to satisfy himself on this point also by first destroying by heat all the fungal forms in a nutrient solution, and then permitting a mould to extend its filaments into it. In this way he kept some solutions thus prepared for four years with only the "mould" form of vegetation in them.

Of the foregoing three groups of organisms the only one which requires to be dealt with here is the third—the *schizomycetes*—as it is only the various forms of this group of the fungal family which have hitherto been unequivocally found in the blood.

Another distinguished botanist, Professor Cohn of Breslau, has also paid much attention to these low forms of life, and has recently devised a new system of classification for them, taking as his starting-point the dictum that the *schizomycetes* are more closely related to *algæ* than to fungi, and suggests, therefore, the term *schizophytæ* for the family, in place of the name given by Nägeli, which has been in general use hitherto. Cohn has, moreover, advanced the supposed differences in physiological properties manifested by some of these low growths as sufficient grounds for assigning to them specific designations. In doing this Nägeli says Cohn has given expression to a generally entertained opinion, and one especially affected by the medical profession; but he (Nägeli) is unacquainted with any facts in support of such a view. "I have," he writes, "during the last ten years examined some thousands of different forms of

fission-yeast cells, but (excluding *sarcinæ*) I could not assert that there was any necessity to separate them into even two specific kinds."[1] On the other hand, there is not sufficient evidence to show that all the forms constitute in reality but one species.[2]

Notwithstanding the circumstances that the *schizomycetes* assume, within certain limits, such different aspects (and the experience of such an authority as Nägeli on such a matter as this cannot be lightly set aside), it is, nevertheless, convenient, irrespective of any particular theories, that terms should be adopted which will suffice to distinguish the leading forms.

Dujardin suggested three terms for the group: (1) *bacterium*, (2) *vibrio*, and (3) *spirillum*. Notwithstanding the great advance which has been made in our knowledge of these organisms since the date of Dujardin's classification, there still remains very much to be done before anything like a satisfactory settlement of the matter can be accomplished. It will, therefore, perhaps be

FIG. 1.—Various forms of fission-fungi—*Schizomycetes*. A, Spherical bacteria (*Bacterium punctum*); B, Elongated bacteria (*Bacterium termo*); C, Vibrions; D, Bacilli; E, Spirilla. × 600 diam.

better for the present to accept these simple terms, especially as, with very trifling modifications, they are sufficient to indicate all the forms which have hitherto been found in the blood. The following brief description will suffice to explain what forms of this group of organisms are comprehended by the terms adopted: 1, *Spherical bacteria*—minute, vitalised bodies, barely visible with the highest powers (fig. 1, A); 2, *Elongated bacteria*—almost equally minute cylindrical rods (fig. 1, B); 3, *Vibriones*—short, undulating filaments manifesting somewhat screw-like movements (fig. 1, C); 4, *Bacilli*, or *Vibrio-bacilli*—fine, short filaments, indistinctly jointed, which, when they attain considerable length, are sometimes described as *leptothrix* filaments (fig. 1, D); 5,

[1] Op. cit., p. 20.
[2] Op. cit., p. 22. Also A. de Bary, 'Ueber Schimmel und Hefe,' 1869.

Spirilla—fine, more or less flexible, spiral filaments, which manifest well-marked screw-like movements (fig. 1, B.).

It may be mentioned, in passing, that examples of each of these forms may commonly be detected in the muco-salivary fluid from the mouth of healthy persons.

The question which naturally suggests itself now is: Under what condition are organisms of this character found in the blood? M. Pasteur states that the blood in health is absolutely free from anything of the kind. His words are: "Le sang d'un animal en pleine santé ne renferme jamais d'organismes microscopiques ni leurs germes."[1] Dr. Beale, on the other hand, says, "The higher life is, I think, interpenetrated, as it were, by the lowest life. Probably there is not a tissue in which these germs are not; nor is the blood of man free from them."[2] It may appear strange that the satisfactory settlement of a question, apparently so very simple, should hitherto have proved impossible, and that many eminent observers should have arrived at opposite conclusions regarding it. It may be that to a certain extent both classes of observers are in the right, for if, as is not uncommonly affirmed, very many of these extremely minute organisms constantly find their way into the circulation through the lungs and pass through the walls of the intestinal tract along with the food (that *bacteria* pass with fluids through a membranous septum is a well-ascertained fact, as also that they will pass through porous earthenware and other filtering media), it is very certain that their existence in the plasma of healthy blood is of comparatively short duration.

This point has been definitely settled as the result of observation by many pathologists, and Dr. Douglas Cunningham and myself were, some years ago, able to satisfy ourselves that *bacteria*, *vibriones*, *bacilli*, and so forth, very speedily disappear from the *liquor sanguinis*, even when introduced into it during life in considerable numbers. Out of forty-nine experiments which were conducted by us with a view of clearing up this matter, twelve of the animals were examined within six hours of the organisms being injected into the veins, and *bacteria*, &c., were found to be present in seven, or at the rate of about 58 per cent.; and out of thirty examined within twenty-four hours, their presence was detected in fourteen, or 47 per cent.; whereas in nineteen specimens of blood derived from animals which had been inoculated in this manner from two to seven days previously, these bodies could only be detected in two of them, or a little over 10 per cent., just 6 per cent. higher than we had observed to be the case out of a number of ordinary preparations of

[1] 'Comptes Rendus,' t. lxxxv, p. 108; 16th July, 1877.
[2] 'Disease Germs,' 1870, p. 64.

healthy blood which we had examined.[1] It is however, obvious that though it is possible that the blood may be constantly replenished with a greater or less number of these organisms, yet they do not accumulate to any great extent therein, and it may be safely affirmed that their presence in appreciable numbers is, judging from experience, incompatible with a state of perfect health. It will hereafter be seen that the same remarks does not hold good as regards parasites of, apparently, animal nature.

It may be affirmed, further, that in certain diseased conditions microphytes are very generally present, though perhaps not invariably, nor is their number coincident with the gravity of the malady. Omitting the cases in which these organisms have been found associated with disease in insects (on account of the difficulty of isolating and clearly identifying such organisms as are found in the blood in these cases from those found in the tissues generally), it may be stated that it has been clearly established that one or other of the forms of fission-fungi have been found in the blood in two diseases, viz. in *charbon*, *mal de rate* or *splenic fever*, and in *recurrent fever*. M. Pasteur has recently maintained that a third should be added to the list—*septicæmia*; and, still more recently, a fourth has been added by Dr. Klein, namely, the disease commonly known as "*typhoid fever*" of the pig.

These matters have, during the last few years, received great attention from thoughtful members of the medical profession, and probably at the present time no subject of a scientific character is being more closely investigated.

The importance of thoroughly sifting the evidence on which the interpretations which have been placed on the significance of such organisms in the blood can scarcely be over-rated, seeing that, should the view now commonly advanced, prove to be correct, the theory and practice of medicine would be radically affected and, possibly, the future action of the State with regard to disease be materially modified. Before making an attempt to institute such an examination, it may be well to refer briefly to the more salient circumstances which have conduced to make the present doctrine of the causative relation to disease of these low forms of plant-life so attractive to botanists and to the medical profession. "The foundations of the germ theory of disease in its most commonly accepted form," writes Dr. Charlton Bastian,[2] "were laid in 1836

[1] Cholera: "A Report of Microscopical and Physiological Researches," Series, I, Appendix A, 'Eighth Annual Report of the Sanitary Commissioner with the Government of India,' 1872.

[2] Paper read before the Pathological Society of London, April 6th, 1875. 'Lancet,' vol. i, p. 501, 1875. 'British Medical Journal,' vol. i, p. 469, 1875.

and shortly afterwards. The discovery at this time of the yeast-plant by Schwann and Cagniard-Latour soon led to the more general recognition of the almost constant association of certain low organisms with different kinds of fermentations. But it was not till twenty years afterwards that Pasteur announced, as the result of his apparently conclusive researches, that low organisms acted as the invariable causes of fermentations and putrefactions; that such changes, in fact, though chemical processes, were only capable of being initiated by the agency of living units." These observations and the interpretations applied to them very rapidly caught the ear of the medical profession, as from a very early period in the history of medicine the supposition that disease was propagated by means of a ferment—a leaven—had taken a firm hold. Previous to the publication of M. Pasteur's observations, a physico-chemical theory had been almost universally acknowledged as sufficiently explanatory of the phenomena manifested by certain classes of disease. This was notably the case with regard to the fermentation-doctrine of Liebig, a doctrine the truth of which he strongly advocated until the day of his death in 1873, and which, somewhat modified as a result of later researches, is still upheld by some of the most eminent chemists of our own time.

The leading features the "vital" and the "physico-chemical" theories of fermentation[1] have recently been lucidly summarised by Mr. C. T. Kingzett in a paper read before the Society of Arts.[2] With regard to the first of these views and in illustration of them this chemist remarks: "When a solution of sugar is exposed to the action of healthy yeast it suffers a change; the atoms comprised in its molecules are broken up and rearranged into new forms, which are recognised as alcohol and carbonic dioxide. Glycerine and succinic acid are also formed at the expense of the sugar, but the lactic acid which generally accompanies alcoholic fermentation is considered as proved to be due to the presence of a ferment distinct from, but accompanying, the

[1] 'Certain organic compounds, when exposed to the action of air, water, and a certain temperature, undergo decomposition, consisting either in a slow combustion oroxidation by the surrounding air, or in a new arrangement of the elements of the compound in different proportions (often with assimilation of the elements of water), and the consequent formation of new products. The former process, that of slow combustion, is called *Erema-causis* or *Decay*; the latter is called *Putrefaction* or *Fermentation—putrefaction* when it is accompanied by an offensive odour, *fermentation* when no such odour is evolved, and especially if the process results in the formation of useful products; thus, the decomposition of a dead body, or of a quantity of blood or urine, is putrefaction; that of grape-juice or malt-wort, which yields alcohol, is fermentation.'—'Watt's Dictionary of Chemistry,' vol. ii, p. 624; 1872.

[2] 'Journal of the Society of Arts,' March, 1878.

yeast. . . . The fermentation alluded to is regarded as a particular instance of a biological reaction, manifesting itself as the result of a special force residing in organisms ; or, in other words, fermentation is essentially a correlative phenomenon of a vital act, beginning and ending with it. On this hypothesis, where there is fermentation there is organisation, development, and multiplication of the globules of the ferment itself. The instance quoted above is by no means solitary; it is exemplary of many other changes, induced by the same or other fermented matters in media suitable for their growth and reproduction. Thus, we have mannitic, lactic, ammoniacal, and butyric fermentations, besides many others, all of them having one feature in common, viz. the reproduction of the ferment.[1] It has not yet, however, been satisfactorily ascertained—a very essential matter to be settled before the foregoing interpretation of fermentative processes can be established—that the several processes are the result of the action of specifically distinct growths.

Baron Liebig vigorously opposed this doctrine, and Mr. Kingzett suggests, probably ignored the influence, of vital action to too great an extent; all that was required in his opinion for inducing the fermentative change was contact with matter which was itself undergoing change. Mr. Kingzett thus sums up the physico-chemical doctrine of fermentation as advanced by Liebig:—Mechanical or other motion exerts an influence on the power which determines the state of a body. Thus, a crystal of sulphate of sodium, a speck of dust, or grain of sand, when dropped into a saturated solution, say of sulphate of sodium, may determine the entire crystallisation of the fluid. Or, again, when fulminates of silver and mercury are tickled lightly by a feather or glass rod, they suddenly explode with violence. A still better instance is the reaction which occurs between peroxide of hydrogen and argentic oxide; these substances, when mixed, give rise to the production of metallic silver and free oxygen; the peroxide of hydrogen, being unstable, is constantly undergoing decomposition from the moment of its formation, and this decomposition results in the production of water and free oxygen; immediately, therefore, that this change comes into contact with oxide of silver, it gives to that body the same tendency to change.

A.—*The Organisms found in the Blood in Splenic Fever.*

On the assumption that certain diseases which are undoubtedly communicable by inoculation, and several others commonly be-

[1] 'Journal of the Society of Arts,' March, 1878.

lieved to be communicable in other ways, are in reality the result of a ferment of some kind, the various theories of the causation of the fermentive processes have always proved an attractive subject of study to the more thinking section of the medical profession. As already stated, the physico-chemical theory of Berzelius, and subsequently of Liebig and his followers, was very commonly accepted as fairly sufficient in connection with the etiology of disease, so long as it was favorably received by the majority of the chemists of the time; but latterly Schwann's views, as expounded and amplified by Pasteur and others, have undoubtedly taken the lead. Probably no single incident has tended so much towards enlisting the attention of the medical profession to it than the publication of the experiments of M. Davaine, which went to show that minute organisms were, to a greater or less degree, constantly present in the bodies of animals which had died of the disease known as malignant pustule in man—the "*Milzbrand*" of Germany; the "*charbon*" of cattle and pigs, and "*mal de rate*" of sheep, in France. The terms "splenic fever" or "splenic apoplexy," "anthracoid disease," &c., are commonly adopted in England in describing the affection. Birch-Hirschfeld[1] states that the organisms found in this affection were first described by Brauell in 1849 and by Pollender in 1857; but, undoubtedly, it was M. Davaine's researches which were the means of drawing serious public attention to the matter. In August, 1850, M. Davaine, in conjunction with M. Rayer, published an account of these organisms, describing them as minute filamentous bodies, motionless, and about double the length of the diameter of a red blood-corpuscle. M. Pasteur[2] maintains that the time just mentioned represents the date of the first publication of the existence of these bodies in charbon, but this idea is manifestly erroneous.

Instigated thereto by the publication of M. Pasteur's researches (which went to show that butyric fermentation was not, as believed, due to an albuminoid body in process of spontaneous decomposition, but to vibriones, which presented the greatest resemblance to the "corps filiformes," found in the blood of animals dying of *charbon*) M. Davaine returned to the subject in 1863 and 1864. The organisms were at first considered by M. Davaine to be bacteria; but finding in certain cases that the filaments or rods varied in length, he modified the name, and they have consequently been, until lately, commonly designated *bacteridia*. At this period it was supposed that they were more closely related to animals than to plants. He satis-

[1] Schmidt's 'Jahrbücher,' Band clxvi, S. 205, 1875.

[2] "Etude sur la maladie charbonneuse;" par MM. Pasteur et Joubert. 'Comptes Rendus,' t. lxxxiv, p. 900, 1877.

fied himself that they were found in the blood during life; that they developed in this fluid and not in the spleen; in fact, he had been able to transfer the organisms to animals whose spleen had been removed. He also ascertained that bacteridia are not found in fœtal blood, although the blood of the mother and of the placenta was crowded with them.[1] The disease was found to be communicable with the food by mixing with it some of the tissues of diseased animals; the effects were less rapidly induced, but the blood became equally affected with bacteridia. He refuses to accept the doctrine of identity of the poison of septicæmia and charbon, on the grounds (1) that the symptoms produced by inoculating animals with putrefying blood are not constantly the same, and that bacteridia do not develop in the circulation of the affected animal; (2) that animals which have swallowed fragments of putrefied tissue rarely died; and (3) that animals which had swallowed fragments of the fresh tissue of animals which had died of septicæmia had been in no way affected. He therefore concluded that the active principle of septicæmia was not regenerated in the animal economy, as in the case of charbon, the latter in fact being a *virus* and the former a *poison*.[2]

In the following number of the 'Comptes Rendus' (p. 429), MM. Davaine and Raimbert announce that they had demonstrated the existence of bacteridia in a man affected with *pustule maligne*, the excised pustule having contained a great number.[3] Portions of this pustule-tissue having being introduced beneath the skin of some animals, the latter succumbed, and after death their blood was found to contain a considerable number of bacteridia.

Such, in a few words, were the observations which drew the special attention of pathologists to this question, and gave marked impetus to the doctrine of disease germs. Since this time very many observations have been recorded, but those of the past two or three years have been particularly valuable from the circumstance that distinct parts of the subject have been taken up by observers peculiarly qualified to deal with the different phases of the extremely complex phenomena which come under

[1] 'Comptes Rendus,' t. lix, p. 393, 1864.

[2] Loc. cit., p. 396. As will subsequently be seen, some of these conclusions are no longer tenable.

[3] Dr. Crisp writes: "As I described in my work on the spleen (1852), dogs, cats, ferrets and pigs, that ate the flesh of these animals, died in a short time, and men that flayed the oxen were affected. In 1832 M. Barthelemy inoculated sheep from the blood of sheep that died of splenic apoplexy, and the inoculated animals died in from thirty-six to sixty hours." —A footnote to the remarks made regarding the 'Germ Theory,' at the Pathological Society, 24th April, 1875.

notice. In the first instance, notice will be taken of the principal observations which are considered to give support to MM. Davaine and Pasteur's views.

In 1875 Professor Ferdinand Cohn published the result of his examinations of these organisms, and having pronounced them to be *bacilli*, suggested that they should bear the name *Bacillus anthracis*.[1] This term has been generally adopted in Germany and England, as, notwithstanding the theory implied in both words, it is convenient to have some such brief designation. Cohn's figure of this bacillus is reproduced (fig. 2), as a

FIG. 2.—*Bacillus anthracis*, obtained, after death, in the blood of an ox which had died of splenic disease. (After Cohn.) × 600 diam.

graphic representation from the hand of so accomplished a mycologist is of special value, and will serve to aid in forming an estimate of the relation of these organisms to others found under other, though somewhat similar, conditions.

In 1876 an important contribution to our knowledge of these organisms was published by Dr. Koch, of Wollstein (Posen), who had had excellent opportunities of studying the disease.[2] Koch had observed that several of the statements and conclusions of M. Davaine had been called in question. Some observers had been able to induce fatal *charbon* by inoculating animals with bacteridial blood without obtaining any bacteridia[2] in the blood of the animal thus affected, although the latter (bacteridia-free) blood had also induced the disease, and, moreover, given rise to bacteridia in the third animal, although none had been present in the second. Others, again, maintained that the disease was not due solely to contagion, but was, somehow, dependent on the soil, seeing that the disease was only endemic in moist, swampy districts, valleys, and sea coasts; and that the mortality was greater in rainy years, and especially during August and September, months in which the temperature of the soil reached its highest. These circumstances could not be ex-

[1] Cohn's 'Beiträge zur Biologie der Pflanzen,' Band i, Heft. 3, 1875.
[2] Cohn's 'Beiträge,' Band ii, Heft. 2.

plained on Davaine's supposition that the organisms, retaining their vitality for a long time in dry air, were conveyed by air currents, or that inoculation was effected by insects, and so forth. Koch's experiments lead him to believe that Davaine's explanation of the mode of propagation of the disease is only partially correct. He found that bacteridia-staves were not so hardy as Davaine had supposed. Blood which contains only rods will retain its property in the dry state for but a few weeks, and when moist only for a few days. How, therefore, could the contagion remain dormant in the soil for months and years? If bacteridia had anything to do with the matter, it must be assumed that during some stages of their development they were inert, or that, as Cohn had suggested,[1] *resting spores* were formed which had the power of retaining their vitality for a long time, and of giving rise anew to bacteridia. The existence of such spores is what Dr. Koch believes he has been able to demonstrate. As this question is a very important one, it is necessary that the evidence adduced should be submitted to careful examination.

The experiments of Davaine and others were repeated, mice having been found to furnish the most satisfactory results. The tail was seized, and a small portion of its skin being abraded, a drop of the fluid containing the bacilli was placed in contact with the small wound. Such inoculations proved to be invariably fatal when fresh material was used. In order partly to ascertain whether the bacilli passed into some other form by successive inoculations, and also to provide himself with a constant supply of fresh material, he inoculated one mouse after another, the last mouse supplying the material for its successor, until eventually a series of twenty inoculations had been conducted; consequently twenty crops of bacilli had been cultivated without any marked change in their character being noticeable.[2] The pathological results were always of the same character—enlarged spleen, and *motionless*, translucent bacilli (fig. 3). The latter in mice were more numerous in the spleen than in the blood, but different animals showed different results as regards their distribution in the tissues—the blood of inoculated rabbits, for example, being often so free from them as to be traced with difficulty, though the spleen and glands contained plenty, whereas in guinea-pigs the number of bacilli in the blood was often so great as to equal, if not exceed, that of the red blood-corpuscles.

On adding a little of the spleen affected with bacilli to perfectly fresh aqueous humour and subjecting the preparation to a temperature of 35–37° C. for from 15 to 20 hours, the bacilli

[1] Cohn's 'Beiträge,' Band i, Heft. 3.

[2] Davaine had conducted a similar series of inoculations.

became elongated to from twice to eight times their original length, and gradually still further increased, till more than a hundred times this length (fig. 4). Some of the filaments now were finely granular, and, here and there, dotted with strongly

Fig. 3.

Fig. 4.

Fig. 3.—*Bacillus anthracis* from the blood of a guinea-pig. Translucent bacillus-rods, undergoing segmentation. Blood-corpuscles are scattered throughout the field. (After Koch.) × 650 diam.

Fig. 4.—*Bacillus anthracis* from the spleen of a mouse after a three-hour "cultivation" in a drop of aqueous humour. (After Koch.) × 650 diam.

refractive molecules, which are believed to be the desired "resting-spores." Very soon nothing remained visible but these 'spores,' as the filament appeared to undergo solution, but the persistence of the arrangement of the former in rows is sufficiently marked to identify them. They will remain unaltered in this state for several weeks.

It will be remarked that the interpretation placed on the character of these refringent bodies clashes with what is so strongly maintained by Nägeli, who, as mentioned already, declares emphatically that the group of lower organisms to which these belong multiply *solely* by fission. It is, therefore, of greater importance to note precisely what the facts adduced are, to prove that in this special instance germinating *spores* are produced.

Dr. Koch states that the fact of his being able to induce splenic fever, together with a plentiful crop of bacilli in the blood, with fluid in which not a trace of bacillus filament is any longer to be found—the minute refractive corpuscles alone remaining, is proof sufficient to show that the latter are [illegible] reality *spores*, and not products of disintegration

merely. Cultivation-experiments were, however, also undertaken, and it was found that in the course of 3 to 4 hours the development of these bodies could be observed under suitable conditions. On careful examination each 'spore' is seen to be an oval-shaped body embedded in a translucent substance which appears to surround the former in a ring-like fashion, but is seen to be in reality spherical, on being rolled over. This substance loses its spherical form and becomes elongated at one end in the direction of the long axis of the contained 'spore.' The latter remains at one end, and very soon the translucent tube assumes a filamentous aspect and, contemporaneously, the 'spore' becomes less refringent, pale, and small, and possibly breaks down into fragments, until it eventually disappears completely.[1] Dr. Koch's figure (fig. 5), representing the various stages of the supposed germination process, is reproduced.

FIG. 5.

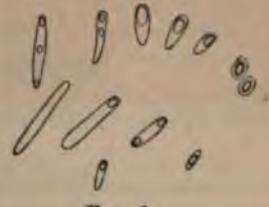


FIG. 6.

FIG. 5.—*Bacillus anthracis:* Germination of the spores (after Koch). × 650 diam.

FIG. 6.—*Bacillus anthracis:* Germination of the spores (after Cohn). × 1650 diam.

This interpretation of what occurs is made particularly important from the fact that it has been resorted to very lately by M. Pasteur to account for the circumstance that, although it has been proved, beyond all reasonable doubt, that splenic fever, together with blood-bacilli, may be induced by inoculation with virus after the total destruction of the filament-bacillus which the morbid material had contained, yet because the 'spores' remained (it would seem that they are considered nearly indestructible) the virus had retained its property—the 'spores' in fact being the virus.

Professor Cohn favoured Dr. Koch with a sketch of the same developmental process as seen under a higher power. This figure is also reproduced for purposes of comparison. Koch suggests that probably the 'spore' consists of a strongly refractive substance, probably oil, which is enveloped by a thin layer of protoplasm—the latter being the substance capable of germination, and the former, perhaps, serving as nourishment during the

[1] Loc. cit., p. 289.

germinating process. The foregoing, according to various writers, represents the complete cycle of development undergone by *Bacillus anthracis*.

Davaine, it will be recollected, had found that animals eating diseased tissues mixed up with their food became themselves affected, and he believed that the spread of the disease could thus to some extent be easily accounted for. Koch, on the contrary, finds that animals very susceptible to infection by inoculation, such as mice and rabbits, may devour such a mixture with impunity. Attempts to inoculate two dogs, a partridge, and a sparrow, proved fruitless.

The latest contribution which has been made towards this inquiry is from the pen of Dr. J. Cossar Ewart.[1] Dr. Ewart confirms Dr. Koch's experiments in many points, and his description of the development of the rods into filaments [fig. 7, and

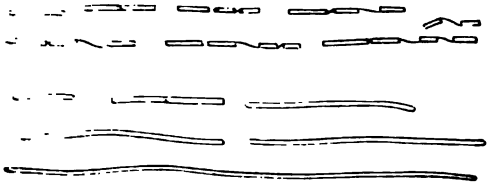


Fig. 7.—*Bacillus anthracis*: Rods undergoing segmentation and lengthening into a filament (after Ewart). × ? diam.

fig. 8 (a)] corresponds with that of previous writers; but his description and figures of the germination of the 'spores' are

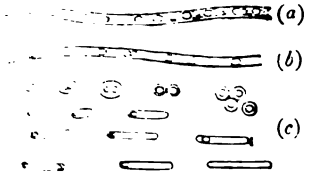


Fig. 8.—*Bacillus anthracis*: (a) A filament containing spores, becoming granular at one end, and showing transverse lines between the spores; (b) part of a filament containing a spore in process of division; (c) shows the different stages through which a spore passes in its development into a rod (after Ewart). × ? diam.

somewhat different. "The spores," writes Dr. Ewart, "when free, according to previous observers, at once grow into rods, and, according to Dr. Koch at least, the rod is formed out of a gelatinous envelope surrounding the spore. My observations

[1] 'Journal of Microscopical Science,' April, 1878, p. 161.

lead me to believe that the spore does not always at once grow into a rod, but that it divides into four sporules by a process of division, in which the envelope as well as the spore takes part. This division I have seen beginning before the spore escaped from the filament [fig. 8 (b)], and that it is not a degeneration is certain, for I have watched the sporules thus formed lengthen into rods [fig. 8, (c)]. Dr. Koch states that the rods are developed from the gelatinous-looking capsule, and not from the bright, shining spore. From what I have seen I think there can be no doubt whatever that the capsule takes no active part during the formation of the rod. The sporule thus slightly elongates (fig. 9), and then from one of its poles an opaque

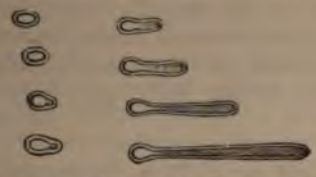


FIG. 9.—*Bacillus anthracis:* A sporule developing into a rod (after Ewart). × ? diam.

process appears, which, as it slowly lengthens, pushes the capsule before it, as it would an elastic membrane. The capsule, as this stretching goes on, becomes at last so thin and transparent that it can no longer be distinguished from its contents."

It is, I think, extremely probable that MM. Cohn and Koch may suggest as an explanation of the discrepancy between their description and figures and those given by Dr. Ewart, that the latter has described and figured the spore (or conidium) of a totally different plant, accidentally present; and MM. Nägeli and de Bary would (in the absence of exact data as to size), in all probability pronounce the germination depicted in the last figure reproduced as being that of a conidium of one or other of our ubiquitous moulds.

Like Koch, Dr. Ewart found that mice could be fed with splenic-disease material mixed with their food without any evil effects ensuing, and that "the spores may be found in the alimentary canal of such mice, sometimes as if in process of development into rods and filaments." With reference to the last remark, a person constantly engaged in microscopic work may question whether it is possible to distinguish these glittering free 'spores' from the myriads of other glistening molecules found in the intestinal canal of all animals.

Contrary to the results hitherto obtained and published by others in support of the view that *Bacillus anthracis* is itself the

specific virus of splenic fever. Dr. Ewart finds that the filaments are not absolutely motionless, but that, at certain stages, they manifest active movements, so that the strongest argument which has hitherto been adduced in favour of these organisms being a peculiar species has disappeared.[1]

Dr. Ewart found also that the bacilli of splenic fever in guinea-pigs differed in size from similar bodies in affected mice, the bacilli of the former being always longer than those of the latter. It was also ascertained that the bacilli and their 'spores' were killed after being boiled for only two minutes, the fluid after this treatment becoming absolutely inert. A like result ensued on similar fluid being subjected to a pressure of twelve atmospheres of oxygen.[2] Considering the position into which the supporters of the germ doctrine had latterly been driven by their antagonists, the announcement made above regarding the instability of the 'spores' will be unwelcome, and none the less so by the circumstance of its having been made by one of their warm adherents.

A few years ago Mons. P. Bert announced that he had ascertained that compressed oxygen rapidly kills all living beings and tissues. He had paid special attention to ferments in the investigations which he had conducted, and had satisfied himself that such of the fermentation processes as were dependent on living matter were immediately suspended when subjected to this influence, whereas those fermentations which were due to some material in solution, such as diastase, pancreatine, myrosine, emulsine, &c., were in no way affected. He then turned his attention to certain poisons secreted in health or disease in animals, the venomous secretion of the scorpion, vaccine matter, &c.[3]

The venom of the scorpion, whether liquid or dried and redissolved in water, resisted the action of compressed oxygen, as was expected, since it owes its activity to a chemical substance akin to the vegetable alkaloids. Fresh liquid vaccine matter was submitted for a week to the action of compressed oxygen, and still retained its power undiminished. Pus from a case of glanders, after being subjected to similar treatment, rapidly killed a horse inoculated with it; hence M. Bert infers that the

[1] Since this was written I have observed that A. Frisch had on three occasions seen independent movements of the staves of *Bacillus anthracis* in blood obtained immediately after the death of the animals, 'Centralblatt für die wissensch. Medicin,' April 7, 1877, p. 247.

[2] Since this was in type a note has appeared in the 'Comptes Rendus,' 15th July, 1878, which confirms this observation. M. Felz found that compressed oxygen, if applied for a sufficiently long period, killed the "germs" as well as the "vibrions" of septic solutions.

[3] 'Comptes Rendus,' t. lxxxiv, p. 1130, May, 1877.

active principle in vaccine and in glanders is not a living being or living cell.

M. Bert then exposed some blood from a case of splenic fever (in which were myriads of bacilli) to the action of compressed oxygen, and found that, although the blood had been exposed in very thin layers, it had retained its virulent properties intact, as was proved by its having killed several guinea-pigs inoculated one from the other, but the blood of these animals did not contain bacilli.

He submitted some other charbon blood containing numerous bacilli to further examination. Some absolute alcohol was very cautiously added to it, drop by drop, until the volume of the original fluid was quadrupled, and the mixture thus obtained was filtered. The coagulum, well washed in alcohol, was rapidly dried *in vacuo*. A fragment of this dried material, on being inserted beneath the skin of a guinea-pig, killed the animal in less than twenty-four hours. The blood obtained from this animal proved fatal to another guinea-pig, as also to a dog. Inoculations were conducted from one animal to another, but the virulent blood of none of these animals contained bacilli.

M. Bert went still further. A watery solution was prepared (by exhaustion) of the alcoholic precipitate, and having satisfied himself that this liquid contained the active principle in solution (for, on the addition of more alcohol, a white flocculent precipitate was induced), three successive inoculations of guinea-pigs were conducted. This rather severe treatment, however, had manifestly diminished the virulence of the material, as inoculation was not successful beyond the third animal, and the material proved too weak to kill a dog.

From these observations M. Bert concluded that the blood in splenic fever contains a toxic and virulent principle, which resists the action of compressed oxygen, and can be isolated in the same manner as diastase.

These observations had been published in an abbreviated form previous to their being submitted to the Academy.[1] M. Pasteur had promptly taken up the subject, and, as he himself was not versed in the medical and veterinary arts, had associated himself with M. Joubert, of the Collége Rollin, for the purpose of more satisfactorily dealing with the matter. Their joint paper[2] was published a few weeks before the publication of the *details* of M. Bert's experiments; it was their remarks, indeed, which led to the latter being published. They obtained charbon blood, and made numerous cultivations of it, transplanting it from vessel to vessel or from animal to animal. Outside the body it was found

[1] 'Comptes Rendus de la Société de Biologie,' January, 1877.
[2] 'Comptes Rendus,' t. lxxxiv, p. 900, April, 1877.

that almost any fluid adapted to the nourishment of minute organisms was suitable to the cultivation of the bacilli—"one of the best and most easily obtained in a pure state being urine made neutral or slightly alkaline." In this way, it is affirmed, poisonous bacilli could be prepared by the kilogram, if required, in the course of a few hours. When the material was filtered, the clear fluid was found to be inert, even though from ten to eighty drops were taken, whereas a single drop of the same unfiltered proved fatal to the inoculated animal; hence it is inferred that the organisms were left behind on the filter, and were the cause of their death.[1]

The foregoing paper was followed by another in July, 1877,[2] by the same authors, in which it is stated that they had repeated M. Bert's experiments, and found that he was perfectly correct as to the destruction of the bacilli, and of the poisonous property of charbon blood at a certain stage under the influence of compressed oxygen, and that, too, even with but a moderate amount of pressure; but that when the bacilli had proceeded to the formation of *spores* they withstood the heat of boiling water, the prolonged action of absolute alcohol, as also the influence of compressed oxygen (= 10 atmospheres for 21 days). The 'spores,' therefore, are most remarkable organisms, seeing that they withstand influences which are destructive to every other form of vegetable or animal life. True, "invisible germs" are accredited with this marvellous power, but, as yet, these 'spores' are the only *visible* bodies for which such persistent vitality has been claimed by eminent authorities. Now, however, that it has been shown by Dr. Cossar Ewart that they are not more exempt from "the tendency to death" than other organisms of a like kind, seeing that they can neither withstand the action of compressed oxygen nor boiling, it is probable that MM. Pasteur, Koch, and their adherents will apply the doctrine

[1] A similar result was obtained by M. Onimus, but the interpretation was very different. M. Onimus found that if the blood of an ox, horse, or person suffering from "typhoid fever," be placed in a dialyser, and the latter placed in distilled water at a temperature of 35° C., a prodigious quantity of organisms would appear, identical in appearance with those in the putrefying blood. But whereas all the animals which were inoculated with a drop of the blood contained in the dialyser died in a short time, those which were treated with the dialysed material (though crowded with organisms) were unaffected. The same result followed when putrefying blood from a rabbit was subjected to similar treatment. Hence M. Onimus infers that the poisonous material is an albuminoid substance, and therefore not dialysable ('Bulletin de la Académie de Médecine,' March, 1873. Cited by M. Ch. Robin in 'Leçons sur les Humeurs,' p. 251, 1874). Clementi and Thin, Schmitz, Bergmann, and others, have obtained more or less similar results.

[2] 'Comptes Rendus,' t. lxxxv, p. 101.

at present fashionable, and aver that, though the "spores" may be dead, their invisible germs still live, and, under favorable circumstances, will reappear.

With the foregoing explanation as to the difference between bacilli and their 'spores,' in their power of withstanding agencies ordinarily destructive to life, M. Pasteur was able to convince his former pupil, M. Bert, of the cause of the discrepancies in their respective results, and this the more readily from the circumstance that when a little of the dried alcoholic precipitate of charbon blood was placed in urine the fluid not only manifested virulent properties, but also gave rise to a plentiful crop of bacillus-filaments identical in appearance with those which had existed in the blood previous to its being treated with alcohol.

It does not seem to have occurred either to M. Pasteur or to M. Bert that under certain circumstances the addition of any dried organic substance to suitable urine would probably be followed by a crop of bacillus. Indeed, it not unfrequently happens that such a crop may be obtained without intentionally adding anything.

Whilst this paper was in preparation it occurred to me to place such a sample of urine under different conditions as to temperature, &c., and to carefully observe the results. Some specimens were made slightly alkaline, others made neutral, and others again left untouched. All the specimens were kept at temperatures varying from 35° to 40° C. (95° to 104° Fahr.), and it was found on the following day that nearly half the specimens were coated with a thin pellicle consisting of bacilli in all stages of development, the spore-stage included, notwithstanding that considerable care had been taken to keep out particles and foreign matter of every description. These appearances are familiar to all who have devoted much attention to microscopic studies. It need hardly be added that organisms thus obtained would produce no effect on animals if freed from the decomposed urine.

B.—*The Vegetable Organisms in Septicæmia.*

The belief that septicæmia is produced by organisms belonging to the lower group of fungi has had almost as many adherents as the doctrine just considered, and the literature in support of it is even more extensive. The virus secreted by animals suffering from this disease is, when transferred to the circulation of other animals, as fatal in its results as that of charbon. It can, moreover, be transferred from animal to animal[1] almost indefinitely.

[1] Observations illustrative of this have long been known. Hamont, for example, in 1827, injected matter from a gangrenous abscess from one horse to another, and from the inoculated horse to a second horse, and found

The symptoms induced by such inoculation are frequently so very like those witnessed in splenic fever that it is often impossible satisfactorily to distinguish them. There is, however, this marked distinction, namely, that whereas the presence of organisms in the blood before death is, to a greater or less extent, the rule in what is known as charbon, it is the exception in septic poisoning. The fluid exuded into the peritoneal cavity, and frequently also into the pericardial sac, is peculiarly prone to give rise to the development of various forms of fission-fungi, and the abundance with which they are sometimes found very shortly after death has given rise to the doctrine that they were the initiatory agencies by which the fatal results were produced.

The publication of Panum's experiments, which went to show that the active morbid principle in such fluids could not by any possibility be vitalised, served for a time to diminish the popularity of such views, but they have since been revived again and again, and never with a greater show of circumstantiality than has recently been the case in a paper submitted by MM. Pasteur and Joubert before the French Academy. This paper, notwithstanding that it exceeded the prescribed length, was, on account of the importance attached to it by the Academy, published *in extenso*.[1]

The paper deals in the first place with M. Bert's experiments, and explains the discrepancies between M. Bert and M. Davaine's results in connection with charbon-blood, as already described. But it goes further than this. It will be recollected that the toxic material submitted to experiments by M. Bert did not give rise to bacilli in the blood, although its virulent properties were most marked, and the possibility of inoculating the disease from animal to animal without bacilli was quite as manifest as in charbon-fluid crowded with them. Similar results have been published by many observers; for instance, MM. Jaillard and Laplat did so very soon after Dr. Davaine's paper was read in 1863, and formulated their conclusion in this wise: (1) charbon is not a parasitic disease; (2) the presence of bacteridia is to be considered as an epi-phenomenon, and not as a cause; and (3) that the fewer bacteridia the blood in *sang de rate* contains, the more virulent it is. It thus became common to hear of cases of charbon with, and cases without, bacteridia.

Davaine has also shown that the virulent properties of the virus of septicæmia manifest a marked increase when transferred from animal to animal. It had been found that after twenty-five such successive inoculations, a millionth, and even a billionth or

that death resulted with pretty much the same symptoms in both cases.—MM. Coze and Feltz in 'Les Maladies Infectieuses,' p. 58, 1872.

[1] 'Comptes Rendus,' t. lxxxv, p. 101, 16th July, 1877.

trillionth, part of the original poison was sufficient to produce death. Rabbits were found to be very susceptible; guinea-pigs somewhat less so. Rats were found to be capable of resisting a considerable quantity. It was also observed by Davaine that decomposing blood lost its virulent properties when exposed to the air in a few days; out of 27 animals inoculated with 1 to $\frac{1}{100}$th of a drop of blood, which had stood from 1 to 10 days, 12 died, whereas out of 26 animals inoculated with like material which had stood from 11 to 60 days only 1 perished.[1]

M. Pasteur, bearing in mind the difference between bacilli of charbon and their 'spores' as regards tenacity of life, determined to ascertain whether a similar condition did not exist in septicæmia. Three animals which had died of charbon were examined —a sheep, dead 6 hours; a horse, dead 20 to 24 hours; and a cow, dead over 48 hours. The blood of the sheep, which had only recently died, contained charbon-bacteridia only; that of the horse bacteridia, together with "*vibrions de putrèfaction;*" whereas that of the cow contained *only* "vibrions" of the kind last mentioned.

Inoculations with the blood of all three animals were followed by death. The autopsies (conducted immediately after death) of the guinea-pigs which had died after inoculation with material from the two last-mentioned animals, revealed extensive inflammation of the muscles of the abdomen and limbs, with accumulations of gas here and there, the liver and lungs discoloured, the spleen normal in size, but often diffluent, the blood of the heart not coagulated, although this characteristic was more evident in the liver—quite as evident as in any case of charbon. Strange to say, writes M. Pasteur, the inflamed muscles contained mobile "vibrions;" these were still more numerous in the serosity of the abdominal cavity, and some of them were of great length.[2] A drop of this fluid would rapidly kill an inoculated animal, but ten or twenty had no effect after it had been filtered. The 'vibrions' are not found in the *blood* till after or very shortly before death, and such blood is said to manifest no virulent properties if taken direct from the heart without contamination with the tissues outside it.

[1] "Inoculation de la matière septique," 'Bulletin de l'Académie de Science,' November, 1872, January, 1873; cited by Birch-Hirschfeld, loc. cit., p. 173.

[2] M. Pasteur, on noticing this condition, asks why it is that a circumstance so general in deaths of this kind had hitherto escaped notice; and replies to the query, that it was doubtless owing to the attention of previous observers having been devoted solely to the blood. It seems strange that M. Pasteur's specially selected *collaborateur*, and adviser in medical matters, did not inform him that this very appearance was about the best known of all the phenomena characterising septic poisoning.

The movements of these "vibrions" were stopped on subjecting them to the action of compressed oxygen, but they were not killed, because on coming into contact with the oxygen they were transformed into *corpuscles-germes*, the 'spores' of Dr. Koch. This, it may be remarked in passing, is a novel and rapid method of producing reproductive elements in plants.

Not only do these "vibrions" of septicæmia withstand the action of compressed oxygen, or rather become transferred by its action from perishable filaments to apparently imperishable *corpuscles-germes*, but they, like the 'spores' in charbon, also withstand the action of absolute alcohol. Hence, M. Pasteur infers that septicæmia, as well as charbon, is caused by organisms—the parasite of the former being mobile, but that of the latter not.

It will be more convenient to analyse these results hereafter.

c.—*Vegetable Organisms in Pneumoenteritis—"Typhoid fever" of the Pig.*

In February of the present year Dr. E. Klein, F.R.S., brought before the Royal Society a portion of the result of an experimental inquiry (which had been conducted for the Medical Officer of the Local Government Board) into the etiology of a disease sometimes described as typhoid fever of the pig, also as hog plague, *mal rouge*, red soldier, and malignant erysipelas. Dr. Klein, however, proposes to show that the disease is not typhoid fever, nor anthrax, but an infectious disease of its own kind, which he proposes to call "infectious pneumo-enteritis" of the pig (*Pneumo-enteritis contagiosa*).[1] The disease appears to present considerable pathological resemblance to septicæmia and to charbon, except that, as regards the latter, the fresh blood does not, as a rule, contain any foreign matter, and in most instances does not possess any infectious property. Of five animals inoculated with the fresh blood, one only was affected, but the specimen of blood which produced this retained its activity when closed in a capillary tube for several weeks. The peritoneal exudation, however, always contains the virus in an active state, and solid lymph obtained from such an exudation will, if dried at about 38° C., prove active. This accords pretty closely with what has usually been observed in septicæmia. Inoculation can also be effected by means of portions of diseased lung, intestine, or spleen, as also with the frothy sanguineous exudation in the bronchi, and infection may take place when the virus is introduced directly into the stomach.

[1] "Experimental Contributions to the Etiology of Infectious Diseases special reference to the Doctrine of Contagium Vivum," 'Quarterly al of Microscopical Science,' April, 1878, p. 170.

It would seem that like organisms were discovered by Leisering some eighteen years ago, in apparently the same affection of the pig as that now described by Dr. Klein.

Dr. Falke, in referring to the bacilli of splenic fever, and after alluding to the circumstance that Delafond had been able to induce the disease in other animals by inoculating them with $\frac{1}{3^{1}_{0}}$th of a drop of bacillus-blood, states that Leisering, in his 'Dresden Report' for 1860, mentions that it is quite correct that such bacilli are found in the blood in splenic disease, but that he (Leisering) had also found that they were present in four pigs which had suffered from well-marked typhus (abdominalis) with ulcers in the intestines and swelled follicles.[1] There is no indication here that the bacilli seen by Dr. Leisering in pig-typhoid differed in appearance from those which he had seen in charbon; on the contrary, he seems to assume that they are identical, and hence questions their being pathognomonic of the latter disease.

Seven cultivation-experiments were conducted by Dr. Klein of the bacilli observed by him "to prove that the virus can be cultivated artificially, *i. e.* outside the body of the animal." Minute portions of peritoneal exudation were added to aqueous humour on a glass side in the usual manner and kept at temperatures ranging from 32° to 39° C. for a day or two; then a portion of the cultivated substance was transferred to a second slide with fresh aqueous humour, and so on till from a third to an eighth generation was reached. With material thus obtained seven animals were inoculated at different stages of the cultivations. All the animals are described as having been affected, but it would appear that death did not result. Doubtless further information as to the symptoms, &c., manifested by the inoculated pigs will be furnished when full details of the experiments are published. In the meantime, it may, however, be noted that it is not mentioned that bacilli were found in the blood of the inoculated animals.

Dr. Klein states that the cultivated liquids proved, on microscopic examination, to be "the seat of the growth and development of a kind of bacterium which has all the characters of *Bacillus subtilis* (Cohn)"—a figure of which, copied from

[1] "Bericht über die Thierarzneiwissenschaft," Schmidt's 'Jahrbücher,' Band 114, p. 131. The original is as follows: "Leisering sagt im Dresdner Bericht f. 1860, dass man nach den vorliegenden Beobachtungen mit Recht annehmen könne, dass im Milzbrandblute diese eigenthümlichen Körperchen stets vorkommen. Er habe jedoch dieselben auch bei vier Schweinen gefunden, welche an ausgeprägtem Typhus litten, der mit Darmgeschwüren, geschwellten Follikeln, blassgraulicher Färbung der Muskeln und keiner Blutüberfüllung der Eingeweide einherging."—Cited by Professor Klob in his 'Pathologisch-Anatomische Studien über das Wesen des Cholera Processes,' Leipzig, 1867.

Cohn's paper, will be found on another page (fig. 13). The rods of the pig-*bacillus* (fig. 10) are referred to as being thinner than those described by Cohn as occurring in hay solutions, also thinner than those of the *Bacillus anthracis*, and, unlike the latter (according to Davaine, Pasteur, Koch, and others), possess a moving stage.[1] It will, however, be recollected that Dr. Ewart has shown that *Bacillus anthracis* may also manifest very active movements. Under favorable circumstances the filaments grow into leptothrix-like filaments (fig. 12) just as other bacilli are known to do.

FIG. 10. FIG. 11. FIG. 12.

FIG. 10.—The Bacillus of infectious *Pneumo-enteritis* of the pig, cultivated in aqueous humour of rabbit, showing spores germinating into rods, isolated rods, and series of rods.

FIG. 11.—From a similar specimen, as in fig. 10, at a later stage; most of the rods have grown into long filaments.

FIG. 12.—Showing the formation of bright cylindrical spores in the filaments at a later stage.

The drawings are represented as the objects appear when seen under a Zeiss's F objective, and Hartnack's III eye-piece, fitted to a Hartnack's small stand (after Klein).

"In these filaments," writes Dr. Klein, "highly refractive spores make their appearance (fig. 12). These become free after the disintegration of the original filamentous matrix. The fully developed spores of our bacillus differ from those of hay-bacillus and anthrax bacillus by being more distinctly cylindrical and much smaller." In a footnote it is mentioned that in the figures accompanying Koch's first paper in Cohn's 'Beiträge' (1876) "the spores are represented in many places as more or less

[1] The letters A, B, used in the original figures (as given in the 'Microscopical Journal'), appear to have become accidentally transposed by the lithographer, as what is referred to in the text under "A, Bacillus of infectious *Pneumo-enteritis* of the pig, cultivated in *aqueous humour*, showing spores germinating into rods, isolated rods, and series of rods," evidently refers to B in the plate, and not to the figure marked A.

spherical in shape;" but if the very valuable micro-photographs of these bodies accompanying Koch's subsequent paper[1] be referred to, it will be found that the 'spores' are very decidedly of a long-oval form. The pig-bacillus 'spores' have according to Klein a long diameter of 0·0005 mm., whereas those of *anthrax* =0·0015—·002 mm. "At first," writes Dr. Klein, "I misinterpreted the spores, regarding them as a kind of *micrococci*, and only after repeated observations have I succeeded in tracing them through their different stages of development." Unfortunately Dr. Klein has not detailed the grounds on which this very important statement is based, nor are figures given. It can scarcely be supposed that any of the figures in the plate are intended to represent the germination of a particular spore. As this distinguished observer well knows, it is not what takes place before the supposed germination, or after it, which has been the subject of debate for so many years in connection with the development of the *schizomycetes*, but the act itself. None of the figures furnished by Dr. Klein present any resemblance to Dr. Ewart's germination-figure (fig. 9) in which the process is unmistakably depicted, but some of them are somewhat like those of Koch (fig, 5); on the other hand, Dr. Klein writes regarding the conclusions of the observer who first ventured to pronounce these bodies in *Bacillus anthracis* to be spores, "I entirely differ from Dr. Koch with regard to the mode of germi- of the spores of bacillus." The points of difference are matters of secondary moment, and need not be specially referred to here.

Dr. Klein concludes his paper thus: "Seeing that splenic fever, pneumo-enteritis, and specific septicæmia possess a great affinity in anatomical respects, and seeing that in splenic fever and pneumo-enteritis there is a definite species of bacillus,—the difference of species being sufficiently great to account for the differences in the two diseases—we may with some probability expect that *also* the third of the group, viz. specific septicæmia, *is due to a bacillus*. This, however, remains to be demonstrated."

Dr. Klein, therefore, believes that whilst the evidence adduced by himself in support of the cause of pneumo-enteritis in the pig being a bacillus is sufficient to warrant a positive statement in the affirmative, that adduced by Davaine, Pasteur, and others in favour of a like cause for septicæmia is not.

[1] Cohn's 'Beiträge,' Band ii, Heft. 3, Taf. xvi, 1877.

D.—*The Vegetable Organisms in the Blood in Recurrent Fever.*

There is one other disease in which vegetable organisms have been found in the blood, namely, recurrent fever (*Febris* or *Typhus recurrens*). In this affection also the organisms belong to the lower fungi-group, the *schizomycetæ*—that is to say, the fungi which multiply by cleavage, in contradistinction to the groups which multiply (1) by sprouting or (2) by germination. The fission-fungi, however, present themselves in this disease in a different form from that witnessed in the preceding, anthracoid, class of affections. In the latter the organisms recognisable range from the spherical bacterium to the bacillus or vibrio-bacillus form—the bacillus being by far the predominating form; but in recurrent fever the representative of the *schizomycetes* is a *spirillum*—a form of the fission-fungi which, so far as I am aware, has not hitherto been detected in any of the anthracoid affections referred to in the preceding pages.

We owe the discovery of this organism in the blood to Virchow's former assistant, the late Dr. Obermeier. They were found in the blood and also in the mouth of persons suffering from this form of fever, and minutely described by him in 1873.[1] It would appear that this observer had already seen them as far back as 1868. In all the cases observed by him they were present in the blood during the height of the fever, but were absent during the remission or intermission, as the case might be; nor were they observed, except rarely, after the crisis. Obermeier describes them as fine fibrine-like threads, equal in length to the diameter of from 1½ to 6 red blood-corpuscles; and manifesting screw-like, progressive movements, which may continue from one to eight hours after removal from the body. The inoculative experiments which he undertook, consisting of the injection of spirillum-blood of fever patients into the veins of dogs, rabbits, and guinea-pigs, proved abortive, nor was there any effect produced by the injection, by means of a subcutaneous syringe, of small quantities of such blood into the bodies of healthy persons.

Obermeier's observations as to the existence of the spirilla in blood in this kind of fever were speedily confirmed by numerous observers, and the negative results which followed his attempts at inoculating persons and animals likewise characterised the attempts of several who followed in his footsteps. Motschutkowsky, however, states that, although he also had failed to inoculate animals, yet he had succeeded in inoculating persons

[1] 'Centralblatt für die medicinische Wissenschaften,' No. 10, March, 1873, and in subsequent numbers during the same year.

with the blood of patients suffering from the fever, no matter whether it contained spirilla or not.[1]

It was, however, soon found that whereas spirilla could generally be detected in cases of fever of this kind, nevertheless cases every now and then occurred in which perfectly competent observers failed to detect them in the blood from first to last, and this too in cases not a whit less severe than those in which the organisms abounded and which were under the care of the same observers during the same period.

Some discrepancy exists in the results of different observers as to the presence of spirilla during apyrexia periods, as well as regards their absence during the height of the paroxysm; Birch-Hirschfeld, for example, observed them two days after the crisis;[2] and Laskousky, basing his observations on thirty-two cases, says that they increase contemporaneously with increase of temperature;[3] whereas Heydenreich maintains that high temperature tends to destroy them—he having found that not only were they most numerous in the blood shortly before the fever was at its height, but that, also, outside of the body they would retain their movements longer in a room at 18° to 21° C. than at a higher temperature. He had been able to keep active spirilla in a preparation from a week to a fortnight at this temperature, whereas the spirilla died in from 15 to 21 hours when kept at blood heat (37°—38° C.). At 40°—41° C. they were found to perish still sooner—namely, in from 4 to 12 hours.[4]

Although, as above shown, they can be preserved alive for a comparatively long time outside the body, nevertheless, every attempt which has been made to 'cultivate' them has proved abortive; no change has been observed to take place in them either in size or in number, notwithstanding that they have been 'cultivated' in media of various kinds and at different temperatures.

B.—*The relation of Microphytes to Disease.*

In the preceding sections the leading facts regarding the connection of living organisms with the occurrence of disease have been detailed; it now remains to consider what grounds there are forbidding the adoption of the doctrine of a germ theory of disease;—why, for example, we should not at once admit that splenic disease is caused by bacteria-rods, and that the aim of treatment should be the destruction of the vitality of those rods; or that recurrent fever is cause by screw-bacteria, and such remedial measures resorted to as tend to destroy them.

[1] Heydenreich, 'Ueber den Parasiten des Rückfallstyphus,' S. 38, 1877.
[2] Schmidt's 'Jahrbücher,' Band. cxvi, S. 211, 1875.
[3] Heydenreich's 'Rückfallstyphus,' p. 39.
[4] Loc. cit., pp. 100 and 101.

[illegible]

[illegible]

[illegible]

various stages in their development correspond in every particular —the only difference which distinguished them being that, whereas *Bacillus anthracis* presented no movements, the bacillus of hay solutions did. This distinction, as has already been stated, has disappeared. Cohn's figure of the hay-bacillus is reproduced

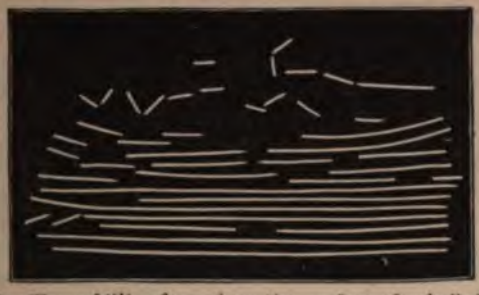


FIG. 13.—*Bacillus subtilis:* formed on the surface of a boiled infusion of hay which had stood 24 to 48 hours (after Cohn). × 650 diam.

(fig. 13), as it may, in the absence of the original paper, prove useful to such as would wish to get a clear conception of what *Bacillus anthracis* itself is like by examining so easily obtainable a substance as a little of the scum which forms on the surface of an infusion of hay.

F.—*The Vegetable Organisms found in Healthy Blood after death considered in relation to the Bacteria and Bacilli of Diseases.*

Several years ago Dr. Cunningham and myself were, whilst conducting various observations together, frequently struck with the rapidity with which organisms appeared in the blood and tissues of animals after death in this country. The microphytes were not limited to minute spherical and elongated bacteria, but there were also present well-marked staves and filaments. In a report submitted by us in 1872, and again in 1874,[1] we drew attention to this matter and suggested the similarity between them and Davaine's bacteridia. A figure of these organisms, which were published by us at the time, is here reproduced (fig. 14)

A short time ago a circumstance occurred which drew my attention again in a special manner to these organisms. Mr. Hart, a veterinary surgeon in Calcutta, forwarded to me for examination a little perfectly fresh blood which he had removed from a horse which had died that day of well-marked anthracoid disease. His curiosity had been aroused as to the microscopical

[1] "Cholera," 'Microscopical and Physiological Researches,' 1st and 2nd series, 1872 and 1874.

characters of the blood by perusing an account, in the 'Veterinary Journal,' of "worms" having been found in the blood of

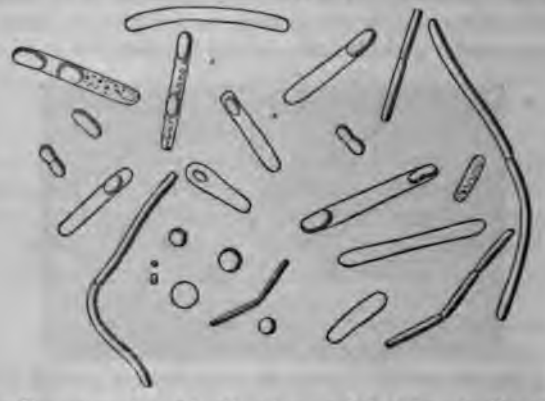


FIG. 14.—Organisms found in the tissues of *healthy* animals a few hours after death. × 1500 diam.

horses suffering from a similar affection in the Punjab. A slide was prepared and examined under the microscope at once, but no marked peculiarity could be detected; but when this and other slides were re-examined twelve hours later, having in the meanwhile been kept under a bell glass, numerous staves and filaments were observed, which, as to size and form, accurately corresponded with the description of like bodies characterising the blood in anthracoid diseases in Europe.

Several "cultivations" were started by adding a little of the blood to fresh aqueous humour. The preparations were then set aside for a few hours in a moist chamber. As the temperature of the atmosphere at that time was generally over 90° F., no special appliances were necessary for supplying artificial heat. The development of the rods into filaments and subsequent appearance of highly refractive oval bodies in the latter corresponded so completely with what Cohn, Koch, Ewart, and others have described, that it is not necessary to give figures of the changes that took place. A series of such cultivations was conducted by transferring a little of the last cultivation to fresh aqueous humour, and so on from one preparation to another.

It was then determined to ascertain whether the bacilli found in the blood of animals which had been set aside for a few hours after death would manifest, under like conditions, similar changes during, their growth. Rats were obtained, killed by means of chloroform, and set aside for from three to twenty-four hours, or longer according as the temperature of the atmosphere was high or low. The result proved that, almost invariably, bacilli were

to be found in their blood, in the spleen, and in other organs. On one occasion the rapid appearance of organisms after death was exemplified in a somewhat remarkable manner, and possibly the mode of death was not without some influence in determining their exceptionally early and plentiful appearance.

The man employed to procure the rats determined that he would get a sufficient number to last for some time, and proceeded to a large granary with his rat traps. Having, however, found that he could procure more than could be accommodated in the cage which he had brought with him, he obtained a large earthen vessel, transferred twenty-seven rats into it, and tied a piece of cloth over the mouth of the vessel. As may be supposed, the rats had perished before he got home—all except one.

I examined the blood and the spleen of twenty of these rats within about six to eight hours of their having been caught, and found in each case that there were innumerable bacilli present, in every way morphologically identical with *Bacillus anthracis*. In some of the cases the number was astonishing. They were present chiefly in the form of rods, but here and there some were seen to have grown to such a length as to cover two fields of the microscope.

This experience tends to give support to the statement made by M. Signol before the French Academy, to the effect that motionless bacilli, identical with those found in charbon, will be found in sixteen hours or less after death in the blood of animals which have been asphyxiated by means of a charcoal fire. M. Signol, moreover, found that eighty drops of this blood would kill a goat or a sheep very rapidly, notwithstanding that putridity could not be detected, so far as appearance and odour went; but that bacilli would not be found in the blood of the inoculated animals, either before or immediately after death.[1]

It has been urged that the microphytes which appear in the blood after death simply make their way into it from the intestinal canal as a result of the breaking down of the tissues. This objection is certainly no longer tenable, for many observers have shown that if some of the organs be removed from the body immediately after death, or, indeed, isolated from the circulation whilst the animal is still alive and under the influence of chloroform, these organisms will nevertheless appear if the preparation be kept for some hours at a suitable temperature.

Some of the specimens of blood which furnished several of the preparations about to be described were obtained in this manner. Rats, mice, kittens, &c., were placed under chloroform, and either killed and placed on one side for some hours; or, whilst still

[1] 'Comptes Rendus,' t. lxxxi, p. 1116, December, 1875.

under the influence of the chloroform, ligatures were passed around the several viscera so as to isolate them before death had taken place. Finally, a ligature was passed around the vessels at the base of the heart, and the organ severed from the body.

The specimens thus procured were repeatedly dipped into either melted paraffin or wax, by means of the string attached to them. In this way they became coated something after the manner of the cotton wick of a candle. Preparations thus made were set aside for from twelve to twenty-four hours, according as the average temperature of the atmosphere was over or under 90° F., and it was almost invariably found that organisms appeared in them, almost, if not quite, as rapidly as they appeared in the bodies of animals which had been simply set aside under like conditions. In the former case, however, the supposition that they were derived from the alimentary canal after death is not possible; nor can it well be maintained that they derived their germs from contact with the scalpel, string, &c., seeing that the entire surface was exposed to the influence of melting paraffin or wax.

The first figure in Plate XVII represents a tracing of a micro-photograph of the bacilli obtained in the manner above described from the blood of a mouse, to all appearances perfectly healthy when killed. A little of the blood was spread in a thin layer on a glass cover and allowed to dry, then a drop of a solution of anilin-blue was added to the slide, so as to stain the micro-phytes, and thus render them more distinctly visible when focussed in the camera. The photographs were obtained by means of a $\frac{1}{16}''$ object glass (immersion), made by Messrs. Powell and Lealand.

When first seen in the blood the majority of these bacilli are motionless—in some preparations completely so, but in others they can be observed to manifest more or less distinctly marked independent movements. They vary in size—in length chiefly—according as their development into filaments has advanced. The average length of each rod is found to be either 5 μ or 10 μ.[1] In the latter case a more or less distinctly marked bend will be recognisable indicative of a joint. In more advanced stages of growth, two, three, or more such joints may be detected, especially on the addition of reagents, such a tincture of iodine. In this case the bacilli will measure either 15, 20, 25, or more micro-millimeters. The length of these segments, whether

[1] μ = micro-millimeter (·001 mm). This mode of stating the measurements is adopted in connection with this series of observations for convenience of comparison with like observations regarding *Bacillus anthracis*. It will be convenient to remember that the average size of a human red blood-corpuscle = 8 μ.

attached or free, varies considerably in preparations from different animals, and even in preparations from the same animal, so that staves may be seen to range from 3 to 6 μ in length and occasionally even to exceed these limits. The average width of the staves was 1 μ, but deviations from the average were equally evident in these measurements also. Sometimes it was found that the specimens present in one organ are smaller or larger than they are in another belonging to the same animal.

If a very minute quantity of blood of this character be placed on a slide with a little aqueous humour, it will be found that in the course of four or five hours, if the temperature be about 90°, the bacilli will have grown very considerably, the majority measuring 20 to 60 μ, and here and there in the preparation a filament may be observed stretching half across the field of the microscope. A few hours later still, a meshwork of well-formed filaments will be manifest (Pl. XVII, fig. 2). Some of these filaments will be found to be distinctly segmented, others apparently without a single segment in their entire length, though even in these a tendency will be observed to form more or less acute angles at certain distances. Other specimens will be found to show traces of segmentation at either end or towards the middle. Drying the specimen, or treating it with reagents, will make the segments much more distinct.

A few hours later some of the filaments will be seen to contain brightly refringent, long-oval molecules, varying slightly in size, but 1·2 μ in length by 1 μ in width, may be given as fair average dimensions. These are the 'spores' which have been described in *Bacillus anthracis*, &c. In a short time these refringent bodies dot the entire length of the filaments, a tendency being manifested to present groups of twos along the line. Gradually the filaments become more and more indistinct, until, finally, only the more or less distinctly linear arrangement of these refringent bodies remains to indicate the path of the filament (Pl. XVII, fig. 3).

I have spent many hours, days even, in watching isolated molecules of this kind, but have never been able to see anything which would warrant my saying positively that they germinated: I can only support what Nägeli, de Bary, and others have persistently affirmed, namely, that the schizomycetes multiply by fission only. The bodies described and figured as germinating by Cohn, Koch, and others (figs. 5, 6) may be seen in most preparations, some of which will be found figured by myself in Pl. XVII, fig. 5, but, so far as my experience goes, none of the objects delineated represent the germination of 'spores' or conidia; certainly, here and there, bodies may be seen which at first sight appear very like it—such, for example, as the refrin-

gent molecule figured at 5*a* as seen by Powell and Lealand's one-sixteenth immersion—but frequently the extremely translucent filament attached to it extends beyond the 'spore' at either end (fig. 5 *b*), thus showing that the filament is not formed of plasma which had proceeded out of the 'spore,' but is, in reality, a tube enveloping it. It has been observed already that the observers who maintain that these refractive bodies germinate base their opinions on different grounds.[1] Their figures in most cases agree, but their interpretations differ.

It may be suggested that, although the bacilli found in the decomposing blood of healthy animals do produce spores, they are not of the same character as the spores found in *Bacillus anthracis*. To this it may be replied that Cohn states that the spores in the latter are identical in appearance and run through the same developmental stages as the spores of the *Bacillus subtilis* of hay-solutions, so that the remarks which I have ventured to make regarding the 'spores' of the bacillus of ordinary blood apply equally to bacillus of hay-infusions, for I have been unsuccessful in witnessing anything like the germinative process in the 'spores' of the latter also. Nor were the 'spores' which formed in bacilli associated with the anthrax blood of the horse observed to germinate.

With regard to specific distinctions which have been based on the differences of size which microphytes of this character present—specific distinctions which, in all probability, will be still further advocated in the future—it is of interest to note that the bacilli found in the blood and tissues of animals which, the period immediately preceding their death, had been perfectly healthy, manifest considerable latitude in this respect. The following extracts from my note book may serve as illustrations of this, and, at the same time, furnish a brief epitome of the changes which bacilli-filaments undergo under very slight varying circumstances. The first series of extracts will refer to bacilli of a smaller size than ordinarily seen. The notes run as follows:—"Killed two mice yesterday and examined one of them to-day, twenty-four hours after death. The red blood-cells from blood taken from the heart fairly well preserved

[1] Since this paper was printed I have seen a very interesting paper by Brefeld dealing with this subject ('Untersuchungen der Spaltpilze,zum ersten der Gattung *Bacillus*'), in which it is maintained that neither Cohn nor Koch could have seen the actual germination of these bodies, as, according to his (Brefeld's) own observations, the process takes place in a different from that described by them. This distinguished botanist states that he has satisfied himself that germination takes place at *a right angle to the axis of the "spore,"* and that the act takes place more rapidly after prolonged boiling. It will be recollected that Dr. Ewart found that the 'spores' were killed after being boiled for only two minutes.

Numerous short bacilli present—motionless. The spleen also crowded with similar bacilli. They appear to be of a smaller size than are usually met with, the segments averaging only 2·5 μ in length by ·8 to 1 μ in breadth; though, in many of the rods, indications of segmentation could not be detected, or detected only in parts of them. The segments became more evident on drying, so that measurements could be accurately made. The sketch opposite has been drawn accurately to scale (*vide* Pl. XVII, fig. 6). A drop of aqueous humour was placed on a cover-glass and a needle dipped into the spleen, and then applied to the droplet of humour. The cover was inverted and placed on a glass slide, hollowed in the centre, a little olive oil having been placed along the rim of the hollow to maintain the cover in its position. Another specimen was prepared and mounted on a slide in the ordinary way (*i.e.* without access to air except along the edge of the cover-glass), and both were set aside until the following day."

The course taken by the latter preparation is described as follows:—"The 'ordinary' preparation of yesterday's note was found to have altered somewhat. At one side of the slide a number of *Bacterium termo* had developed, forming a whitish rim; along with these were staves of the same character as described yesterday, but considerably grown, which were being knocked about in all directions by the bacteria. The greater portion of the preparation had gone on to 'spore' formation, as figured at *a*, Pl. XVII, fig. 7. In others the filaments and joints were still distinct and presented a protoplasmic aspect (*b*). Many of the filaments were held together by very slender cords, sometimes as if by one corner only, probably owing to a twisting of the tube; at others the continuation of the tube was distinct (*c*). [Compare this description with the figures of *Bacillus anthracis* reproduced from Dr. Cossar Ewart's paper, fig. 7 and 8.] Here and there filaments could be seen in a transition stage, a 'spore' having formed in each segment, the joint being still faintly visible, but the plasma disappeared except at one or two parts—generally the end segments of a thread. Commonly the separated segments contained two 'spores,' presumably coinciding with the original number of segments. The threads are wider when containing 'spores' than previously. The 'spores' = 1 to 1·4 μ in length, ·8 to 1 μ in breadth. The space allotted to each 'spore' in a filament, presumably each segment, was from 6 to 7 μ in length, so that a filament containing 2 'spores' would equal 12 to 14 μ, and 3 'spores' = 18 to 21 μ, and so on, so that the filament manifestly swells out in all directions."

The third day: "Having set the slide in moist air under a

bell-glass, evaporation was prevented. Not much change has taken place, except that here and there is seen that some of the 'spores' within the filaments present a longer appearance, and have become correspondingly narrower. In some a constriction is seen, and others are completely divided and form two complete molecules (Pl. XVII, fig. 8). In some instances the molecules had become separated. [Compare with Dr. Ewart's figure of *Bacillus anthracis*, fig. 8.] That the refringent particles were in reality the 'spores' of the previously distinctly seen filaments was evident from the circumstance that, although the hyaline tube which contained them was extremely translucent and only with difficulty brought into view, still it was sufficiently strong to be able to retain these refractive molecules in a row; any movement communicated to one part of the row was seen to be accompanied by movement of the entire series. The movements were caused by the constant agitation of objects in the field on account of the presence of *Bacterium termo*."

No further change could be detected in the 'spores.'

The foregoing description, though applying to the more generally observed appearances which bacillus growths present, is by no means the only course taken by such organisms when transferred to nutritive media other than that in which they were developed, nor is it by any means a matter of certainty, at starting, what particular course will be followed by them. In illustration of this and also of the fact that, occasionally, exceptionally large bacilli are to be found predominating in the blood (just as we have seen to be the case with regard to exceptionally small ones), the following extract from my note book may be instructive:—A rat which had been killed at 10 o'clock in the morning was dissected at 5 in the afternoon of the same day. The temperature had been about 94° F. The heart was carefully taken out and a minute quantity of blood transferred, on the tip of a scalpel, to a slide. A small quantity of a half per cent. solution of salt and distilled water was added, in order to dilute the preparation, and, by separating the corpuscles, render it easier to see any foreign matters that might exist in the serum. There were numerous motionless bacilli varying from 4 to 20 μ in length by ·8 to 1·4 μ in width, the thicker variety predominating (Pl. XVII, fig. 9). The majority consisted of short stiff rods, 5·5 μ in length, or double this length; in the latter case often manifesting indications of a tendency to bend towards the centre. There were also a few thicker rods than these scattered throughout the preparation. An hour having been spent in the examination of this slide, it became apparent that the bacilli were more numerous on it than when the examination commenced. It was then set aside in a moist chamber.

A similar slide was prepared, consisting of just a trace of the

blood mixed with fresh aqueous humour, and placed in the same chamber.

On the following morning this slide, to which the half per cent. salt solution had been added, was re-examined, and it was found that the filaments had grown greatly in length and somewhat in thickness (Pl. XVII, fig. 10); in some instances the filaments extended across the field of the microscope. All the filaments were motionless and almost translucent, quite devoid of granularity, and it was only in some places that a joint could be distinguished. No refringent molecule appeared in any of these long filaments, but there were some short, pale, transparent rods rolling about in the preparation, and in these glistening bodies were found (Pl. XVII, fig. 12). Some of these rods, or segments, were 8 μ long and contained a bright blue (as seen with Hartnack's No. 9 immersion objective) 'spore,' 2 μ in length by 1 μ in width, and other segments, about the same length, contained two. Mixed with these were short, translucent staves, with a distinct joint, some with two 'spores,' separated by a partition, and others shorter (4·5 μ) with only one. By the next day the filaments were broken down and the preparation consisted chiefly of a multitude of active *Bacterium termo*.

The other slide, which had been prepared with aqueous humour, was likewise examined on the following day. The filaments were not so long as in the other preparation, and there appeared to be a decided tendency towards cleavage into small cuboid pellets of plasma (Pl. XVII, fig. 11, *a*). Some of the filaments, though well preserved at one end, were seen to be undergoing the process of fission at the other, each fragment being equal to 1—1·2 μ in its longest diameter. It seemed as if the 4 to 5 μ-segments, of which the filaments were composed, had first become freed from the thread, and had, instead of giving rise to a 'spore,' undergone fission (fig. 11, *b*). In other cases cleavage of this kind took place whilst the individual segments maintained their linear arrangement (fig. 11, *c*). In some instances it seemed as if the two first halves of the originally 4 to 5 μ-segments had each become elongated (and correspondingly thinner) and undergone further division, thus forming four more or less spherical plastides (fig. 11, *d*). When the whole filament had undergone such a process and the plastides had retained their linear arrangement, it presented the appearance of a rosary chain (fig. 11, *e*). It was ascertained that four of the plastides forming a part of the particular chain sketched were equal to the length of one of the segments of the original filament, viz. 5 μ.

It will thus be seen that filaments of bacilli may disappear at least in two ways: (1) by giving rise to minute highly refractive, long-oval molecules, the filaments themselves becoming at first

transparent, and then, apparently, disappearing more or less completely; and (2) by undergoing cleavage, and giving rise to minute plastides. These may, occasionally, be observed to present a rosary-chain arrangement, but usually their identification becomes impossible owing to their mixing with other molecules in the field.

I am not in a position to offer any suggestion as to which is the normal course for bacilli to take, seeing that bacillus-filaments may redevelop under suitable conditions from material derived from preparations in which either of the two foregoing processes has been observed to take place. Probably, to a greater or less extent, both processes occur together; at least it is seldom that filaments will give rise to the bright, refractive molecules, in a highly nutritious fluid, without a contemporaneous formation of plastides taking place at some part of the preparation.

6.—*The relation of the Spirillum of Recurrent Fever to other known Spirilla.*

Having thus endeavoured to prove that no sufficient grounds have been adduced for accepting the doctrine that bacilli have been found in splenic disease, septicæmia, and so forth, which differ, not only in any *material* respects, but in any respects whatsoever, from bacilli which may be found under certain easily induced conditions, it remains to be seen what evidence there exists to show that the other member of the schizomycetes group found in recurrent fever—*Spirillum Obermeieri*—differs from other spirilla known to be harmless.

On this point also considerable diversity of opinion exists, though perhaps not quite to so marked an extent as with respect to the microphytes which have just been considered. The matter is, moreover, made somewhat simpler from the circumstance that those who have had the greatest opportunities for personal observation are, on the whole, the observers least inclined to claim for this spirillum specific characters in the ordinary botanical sense of the term.

Since the period of its discovery in the blood by Obermeier it has been referred to under various names: *Spirothrix, Protomycetum recurrentis,* in Lebert's article on recurrent fever and in Ziemssen's 'Handbuch' of Medicine; *Spirillum* by Erichsen, Litten, Birch-Hirschfeld, &c.; *Spirillum tenue* by Naunyn; and *Spirochæte Obermeieri* by Cohn (fig. 15).

The last-named observer, and the only one with an extended botanical experience, gave it a specific distinction solely on physiological grounds, as, after careful examination, he was unable *to detect any difference, either in size or in character of move-*

ments, between the spirillum of recurrent fever-blood and *Spirillum* (*Spirochæte*) *plicatile*, which had been found by Ehrenberg in water many years ago.[1] Cohn himself had subse-

Fig. 15. Fig. 16.

Fig. 15.—*Spirillum* (*Spirochæte*) *Obermeieri*. The spirilla among blood-cells * * in active movement. Those marked * sketched a short time before the cessation of the fever (after Weigert; published by Cohn). × 600 diam.

Fig. 16.—*Spirillum* (*Spirochæte*) *plicatile* (after Cohn). × 650 diam.

quently found it in water, and *also* in the mouth—in the mucus surrounding the teeth.[2] A figure of this spirillum by Cohn is reproduced for convenience of comparison[3] (fig. 16).

It will be recollected that the late Dr. Obermeier himself had recognised the spirillum in the mucus from the mouth of recurrent fever patients, possibly having overlooked the circumstance that its presence in this fluid was not an abnormality. Manassein,[4] who, at St. Petersburg, has had favorable opportunities for observation, expresses himself most strongly against the supposition that this microphyte is anything more than an epiphenomenon in recurrent fever. Not only was it absent from the blood in certain of the cases of fever examined by himself and others, but spirilla precisely similar to those found in other cases were, during a period of some months, constantly present in the secretion which flowed on pressure from an abscess which

[1] Cohn's 'Beiträge,' Band i, Heft. 3, 1875, p. 197.

[2] Ditto, Band i, Heft. 2, 1872, p. 180.

[3] Ehrenberg suggested that the term *Spirillum* should be restricted to such of the Schizomycetes as manifested spiral movements without flexibility, and for those of the group which were distinctly flexible he proposed the term *Spirochæte*. As, however, the distinction is merely a matter of degree, spirilla also manifesting a greater or less amount of flexibility, I have adhered to Dujardin's classification. Fomental ('Etude sur les Microzoaires,' 1874) adopts the older and simpler term for a like reason.

[4] 'St. Petersburg. medicin Wochenschrift,' No. 18, 1876.

opened into the mouth of a fever-free patient. Billroth also states that similar spirilla were found in connection with caries of bone.

Heydenreich, who probably has investigated this matter as carefully as any observer, and written the fullest account of it which has come under my notice, notwithstanding his manifest desire to claim for the spirillum a causative relation to the disease, is, nevertheless, compelled to own that sufficient reason has not been shown to warrant its being described as specifically different from the spirillum of water and the ordinary spirillum of the mouth.[1]

In May, 1877, I had an opportunity of observing cases of fever in Bombay in which Dr. Vandyke Carter had demonstrated the existence of spirillar organisms in the blood. Dr. Carter has recently published an interesting account of his observations.[2] These, as far as the abstract of the paper submitted to the Pathological Society shows, coincide closely with like observations in Europe. During my stay in Bombay I had an opportunity of examining twenty-five cases of the disease, and observed the spirillum in five of these on several occasions. It could not, however, be said that the other subjective symptoms in these cases were more grave than in other cases of the fever, in which not a trace of the spirilla could be found.

One of the preparations of blood, containing these organisms, which I was able to preserve, is a particularly good one, and as it was obtained by exposing the fluid immediately on its removal to the fumes of a weak solution of osmic acid, it may be considered as representing the spirilla exactly as they appeared in a perfectly fresh slide. The fumes of this acid, as has been stated by several observers, are particularly useful in preserving the natural appearance of these microphytes, as, indeed, of blood preparations generally. Professor Ray Lankester, when recommending its use to English observers, wrote: "It is sufficient to expose a thin film of blood on a glass cover to the vapour arising from a bottle containing a two per cent. solution of osmic acid, during three minutes, to ensure its complete preservation. Every corpuscle thus becomes 'set,' as it were, in its living form; there is no coagulation, no shrinking, no dissolution; but as the corpuscle was at the moment of exposure to the vapour so it remains. The white corpuscles even exhibit their pseudopodial processes arrested in the act of movement. It is as though the osmic-acid bottle contained a Gorgon's head, which freezes the corpuscles, as they face it, into stone."[3]

I have prepared several micro-photographs of this slide in the

[1] Op. cit. p. 31.
[2] 'The Lancet,' June, 1878.
[3] 'Quarterly Journal of Microscopical Science, vol. xi, p. 370, 1871.

hope of being able to supply facsimile copies of some of them with this paper. I fear, however, that it will not be practicable to obtain reproductions of the negatives by any of the permanent photographic processes practised in Europe in sufficient time to permit of their publication at present. I have therefore caused tracings of some of the leading forms to be made and have had them engraved on wood (fig. 17).[1]

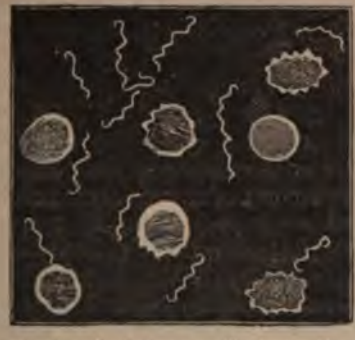


FIG. 17.—Spirilla in the blood of fever patients in Bombay; traced from micro-photographs taken with Ross' $\frac{1}{12}$" immersion objective. Some of the longer spirilla in the woodcut are in the micro-photographs seen to consist of two fibrils loosely attached at the ends. This peculiarity cannot be reproduced in the engraving. Several of the blood-corpuscles present a stellate appearance.

In the last number of Cohn's 'Beiträge' (Band II, Heft 3), Dr. Koch has supplied some excellent micro-photographs of the spirilla as observed at St. Petersburg. The spirilla in the osmic-acid preparation which I possess, though presenting the same general characters as those in Dr. Koch's photographs, are somewhat thicker than those depicted in the latter; whether this points to any slight difference in the blood between the fever which prevailed in Bombay last year and the fever which prevailed in St. Petersburg I am not prepared to say, but this much, I think, I may venture to state, namely, that the difference between the spirilla in the preparation in my possession and those received from St. Petersburg, as photographed by Dr. Koch, or the spirilla sketched by Weigert (fig. 15), is as great as the difference which exists between the *Spirillum Obermeieri* and the *Spirillum plicatile*, on the one hand, and the *Spirillum* of the mouth on the other. As has already been seen, these differences are exceedingly trivial, and it is quite possible that such slight differences may exist in these microphytes in different persons during the same epidemic, and at different

[1] Two of these micro-photographs will be found reproduced as permanent photographs, by the Autotype Company, in the original memoir.

times in the same individual, as has been shown to be the case in the preceding pages with regard to the bacilli in the blood.

It may be useful to say a few words, in passing, regarding the fever which was so prevalent in Bombay during a great part of 1877, as some misapprehension appears to exist as to its exact character. What is described as recurrent fever, and sometimes as bilious typhus or bilious remittent fever, and recurrent typhus, in Germany, is frequently assumed in England to be the same as the "relapsing-famine fever," which was witnessed some years ago in Ireland and elsewhere. Whether in reality the latter fever was or was not the direct offspring of want is not a matter calling for comment here, but what is very definitely known is that outbreaks of recurrent fever in various parts of Russia and Germany, and which were found to be associated with spirilla in the blood, have occurred in districts wholly unassociated with want of any kind. In some cases, indeed, the outbreaks occurred in districts and during periods in which the labouring classes were exceptionally well off. This is a point concerning which no doubt whatever can exist. With regard to the supposed connection of the fever in Bombay with the famine which prevailed in certain parts of the country, I can only state that, so far as I could gather as the result of personal observation and careful inquiry, no sufficient grounds existed to warrant any such supposition; and Surgeon-General Hunter, after a most careful analysis of the official records, and writing from personal acquaintance with the disease, thus sums up his report on this particular point: "Any distinct causal connection, therefore, between the famine and the fever must be abandoned."[1]

It thus follows that the term "relapsing-famine fever" is not applicable to the affection hitherto associated with spirilla in the blood, whether in Germany, Russia, or Bombay.

II.—*The probabilities in favour of the Bacilli and Spirilla of the Blood being Epi-phenomena.*

There is one circumstance in connection with the microscopic appearance which these organisms sometimes present which deserves special mention, as it may serve as an explanation of their sudden disappearance from the blood; and that is that they may present a well-marked beaded or rosary chain appearance (fig. 18). This feature I was able to observe on one occasion only. The spirilla of the ordinary character were plentiful in this person's blood on the evening previous to the day on which this observation was made, but when examined on the following

[1] 'Indian Medical Gazette,' October 1st, 1877.

morning there were only linked or rosary-chain spirilla in his blood. They were not very numerous, and their movements were not of that *rushing* character ordinarily observed, but conveyed the impression of *tumbling* across the field.

FIG. 18.—Beaded or rosary-chain appearance assumed by the spirilla found in the blood of a fever patient at Bombay (sketched as seen by Hartnack's immersion objective No. 9, ocular 4).

The inference which such an observation appears to warrant is, that when the blood acquires a certain as yet undetermined condition it becomes unadapted to the existence of spirilla, and that the fibrils thereupon undergo segmentation, after the manner of other schizomycetes [compare with fig. 11, Pl. XVII], and the separated plastides become diffused throughout the circulation; possibly, they then gradually disappear in the same manner as we have seen other plastides (minute bacteria, &c.), disappear very rapidly after being injected into the circulation. This appears to me to be more probable than that they continue in the circulation until the blood reacquires the state suitable to their growth into fibrils, seeing that the time for their return is so uncertain —it may be two days, may be six days, or a fortnight even, and perhaps they may not return at all. Be that as it may, it is clearly evident that their existence as spirilla is dependent on the composition of the fluids of the body.

Heydenreich suggests that their disappearance is due to the elevated temperature of the blood at the height of a paroxysm. If that were the case, they ought to become more numerous with the fall of temperature after death, but it is well known that they disappear exceedingly rapidly when life becomes extinct, in this respect offering a marked contrast to other members of the cleft-fungi group—bacteria and bacilli.

The fact of their total disappearance immediately after death, probably even before death actually takes place, is very significant, as showing the extremely close relation which exists between them and the blood in *living* tissues, seeing that when the blood is removed from the body the spirilla will, under favorable conditions, retain their power of locomotion for several hours or days. What these subtle changes of the blood during fever pro-

cesses may be, chemistry and physiology have not yet revealed; we can therefore only judge of them by the changes of the temperature, &c., of the patient; and, in the particular condition under consideration by the occasional appearance and reappearance of spirilla, whose presence is manifestly dependent on antecedent changes. That the temperature commences to rise and that other subjective symptoms are manifested before the appearance of spirilla testifies to this, for it cannot be that they can exert an influence before they are themselves existent.

Dr. Charles Murchison, at the discussion on the germ-theory of disease at the Pathological Society,[1] put this matter very clearly when he said: "The fact that in relapsing fever and sheep-pox distinct forms of bacteria have been found in no way proves any casual relationship between these diseases and the bacteria, and is readily accounted for by the acknowledged fact that the form taken by many minute growths depends not upon the germ, but upon the nature of the medium in which it grows. Indeed, the observations which have been made on the spirilla of relapsing fever are strongly in favour of this view, for they are present in the blood during the first paroxysm, but disappear before the crisis; are absent during the intermission, but return with the relapse of fever, and again disappear before the crisis. It seems difficult to account for their appearance and annihilation twice over, except on the supposition that the soil was suitable for their development during the febrile process, and unsuitable when the febrile process was complete." The remarks which Dr. Bastian made in opening the same discussion on his very interesting observation as to the presence of bacteria in the fluid of a blister-bleb of a febrile patient so long as the bleb remained intact for forty-eight hours, whereas in the fluid of a blister from a healthy person no such appearances would be seen, point in the same direction.

A like conclusion must be arrived at regarding the bacilli in malignant pustule, septicæmia, and the so-called "typhoid fever" in the pig, horse, and other animals. With regard to the microphytes just named, it may be confidently stated that they are never to be detected in the earlier stages of the disease, but only at a brief period before and after a fatal termination. To my knowledge they have never been found in the blood of animals which have subsequently recovered; they have always been recognised only as one of the concomitants of impending dissolution. This is undoubtedly the case so far as the two diseases first cited are concerned, and judging from what is known regarding them, I presume that the development of such organisms in the blood of the inoculated pigs was not one of the symptoms

[1] 'The Lancet' and 'British Medical Journal,' April, 1875.

which Dr. Klein had observed as indicative that the bacilli which had been introduced into the system of the animals had induced the disease. Should this inference prove to be correct, it is somewhat difficult to understand on what grounds so emphatic an opinion could have been expressed as to their specific action. It does not appear that Leisering in his account of like organisms, in apparently the same disease of the pig (as already mentioned), had found them in any but fatal cases.

1.—*The evidence which has been adduced showing that the virulence of Septinous Substances is not dependent on vegetable life.*

Seeing that so much evidence can be adduced to show that these organisms, whether bacilli or spirilla, are but epi-phenomena, *the specific change in the fluids of the body having taken place before the slightest indication of their presence can be detected*, the question which naturally suggest itself is: whether sufficient evidence exists to show that inoculations can be effected with like material in the absence of such living organisms. The reply to this question, so far as anthracoid and cognate diseases are concerned, is distinctly in the affirmative; but, with regard to recurrent fever, it cannot be as yet definitely stated that the malady is inoculable, so that for the present it may be left out of consideration.

When Brauell published his paper in 'Virchow's Archiv' in 1858, detailing his experiments to prove that splenic fever was an inoculable disease, he further stated the opinion that the organism found in the blood could not be the carriers of the virus, seeing that blood not containing bacilli had been found to generate the disease. Bouley has arrived at a similar conclusion, and Bollinger, who has repeated Brauell's and Bouley's experiments, has also shown that the disease may exist without the presence of bacilli in the blood, that such blood will induce the disease in other animals, and that even under such circumstances organisms may develop in the blood of the inoculated animal, and be detected during life as well as after death.[1]

Similar observations have been made with regard to septicæmia and the allied disease-conditions associated with the presence of bacilli, some of which have been already referred to. M. Colin, for example, found that $\frac{1}{100000}$ of a drop of septicæmia-blood would kill a rabbit in 36 hours when inoculated by means of a lancet; that the virulent property existed before the appearance of rod-bacteria; and that the pernicious character of the fluid

[1] O. Bollinger, 'Zur Pathologie des Milzbrandes,' München, 1872. Quoted in 'Schmidt's Jahrbücher,' Bd. clxxi, p. 205, 1875.

became evident contemporaneously with the advent of very minute spherical bodies, the consequences, as Colin believes, of the altered character of the blood.[1]

It has been repeatedly demonstrated that the poisonous properties of septinous blood and of other decomposing animal solutions gradually disappear towards the third or fourth day, a fact which is scarcely reconcilable with the doctrine that the poison resides in the apparently almost imperishable 'spores' of the bacilli which existed during the earlier stages of decomposition. A like feature characterises the virus of splenic disease, of small-pox, and of syphilis. Hiller,[2] in summarising the results of filtration of septinous fluids, writes that the most decisive experiments have demonstrated that after filtration through finely porous material, such as charcoal, porous earthenware, compressed wadding, &c., until the fluids have been shown to be absolutely free from visible molecules of every description, they are, nevertheless, still competent to induce all the symptoms which characterised their action before such filtration. These results Hiller says, were arrived at by Panum, Bergmann, Weidenbaum Wolff, Küssner, and others.

To the first-named of these observers belongs the merit of having contributed some of the earliest and most valuable observations which have been, hitherto, recorded in connection with the nature of the poison existing in certain solutions of decomposing animal matter. Panum's researches were published so far back as 1855, but having originally appeared in Danish they had for several years been to a great extent overlooked. They were brought more prominently into notice on their publication in 1874 in 'Virchow's Archiv.' In 1875 [3] Dr. Cunningham and myself drew attention to these experiments, as we have found that the results of observations made by us, with a like object, based on a series of experiments which included the inoculation and dissection of about 170 dogs, were, in so far as they were comparable, almost in complete accord with those which had been obtained by this distinguished experimentalist.

Panum found that the coagulum produced by boiling a septinous fluid was more virulent than the fluid itself. The principal facts demonstrated by him may be thus summarised :—

(1)—That the perfectly clear fluid which may be obtained by filtering solutions of putrefying animal substances through several

[1] "Nouvelles recherches sur l'action des matières putrides et sur la septicémie." 'Bulletin de l'Académie,' October, 1873; cited by Birch-Hirschfeld, l. c., p. 174.

[2] "Ueber putrides Gift," 'Centralblatt für Chirurgie,' Nos. 10, 11, and 12, 1876.

[3] 'Cholera: Microscopical and Physiological Researches,' Series II.

layers of filtering paper would induce the characteristic symptoms of the same kind as the unfiltered material.

(2)—That boiling such a fluid for even 11 hours would not materially impair its toxic properties.

(3)—That although an alcoholic extract of such a fluid proved to be inert, the virulent action of a watery extract of the same fluid was very intense.

Panum therefore concludes that a fluid which can retain its specific property after being filtered, boiled, evaporated to dryness, and the residue digested in cold and in boiling alcohol, then re-dissolved and again filtered, cannot owe this property to living organisms of any kind.

In 1865 Dr. W. B. Richardson showed that the sero-sanguineous fluid from the peritoneal cavity of a person suffering from pyæmia would communicate fatal disease from one animal to another in a direct series, and that the poison (designated "septine") which effected this could be made to combine with acids so as to form salts which retained the poisonous qualities of the original substance.[1] A few years later (1868), Bergmann succeeded in obtaining apparently a similar substance and named it *Sepsin*.[2] This poison induced symptoms of a like character to what are induced by putrefying solutions, and was frequently even more fatal, in very small doses. Still it appears to reproduce symptoms exactly similar to the original material, in this respect differing slightly from Panum's "putrid extract," which reproduces the ordinary symptoms of septic poisoning without any modification whatever.

To Pasteur and his adherents, who ascribe what may be almost termed supernatural powers of resistance to the "resting spores" of anthracoid and other diseases, the facts adduced in the foregoing paragraphs can carry but little weight. But another series of phenomena have been recorded which point in the same direction. It has been shown that the living tissues of the body will under certain conditions, when irritated by means of purely chemical irritants—such, for example, as a strong solution of iodine or liquor ammonia—secrete a fluid which, when transferred from animal to animal, proves not one whit less virulent in its properties than an exudation which has resulted primarily from the introduction into the system of material which has swarmed with bacilli. Observations to this effect have been published by many observers, and Dr. Cunningham and myself have placed on record that we found a large number of bacteria in the blood of a dog which had died as a result of such chemical irritants.

[1] 'The Lancet,' April 3rd, 1875, p. 490.

[2] 'Centralbl. f. d. medicin. Wissensch.,' 1868, p. 497; cited by Dr. Arnold Hiller, op. cit.

These bacteria could not have been the cause of death, nor, most assuredly, could they have derived their origin from the liquor ammonia which had been resorted to to excite the inflammatory process.

It would seem from these results that the living tissue elements of the body itself play a much more important part in the elaboration of septinous and allied poisons, than what has been of late ordinarily ascribed to them.

Such, so far as I have been able to learn, are the main facts which have been recorded with regard to the microphytes of the blood in health and in diseased conditions.

CALCUTTA;
August, 1878.

OBSERVATIONS *on the* GLANDULAR EPITHELIUM *and* DIVISION *of* NUCLEI *in the* SKIN *of* NEWT. By E. KLEIN, M.D., F.R.S. (With Plate XVIII.)

IN number 17 of the 'Centralblatt f. med. Wiss.,' 1879, I have described giant nuclei of the huge epithelial cells lining the large saccular glands of the skin—tail—of newt (*Triton cristatus*). I have shown that these nuclei, when examined fresh in aqueous humor of frog, show an exceedingly distinct network of more or less uniform fibrils and trabeculæ; owing to the large size of the nuclei their network can be seen in all its details even under a low power. Many of these giant nuclei show in the network of the highly refractive fibres and trabeculæ cylindrical or irregular accumulations corresponding to nucleoli, others are free of them. I have also shown that both the nucleoli, when they exist, and the fibrils and trabeculæ, possess vacuoles; and further, that on the warm stage the intranuclear network shows contraction, whereby the outline of the nucleus changes in a similar manner as in cells while undergoing amœboid movement.

Of the gland cells themselves I have mentioned that they likewise show amœboid movement, in the course of which larger or smaller knobs are pushed out, which become withdrawn or constricted off altogether, and then move independently. These cells are also in other respects remarkable, viz. that they are capable of ejecting their nucleus (the above giant nucleus), and after this continuing their movement. Some of them are filled with discoid or spherical fat molecules of various sizes, and they are capable of ejecting

with a sudden jerk the whole or part of their fat molecules and continuing afterwards their amœboid movement. The above giant nuclei vary considerably in size, the smallest being 21 by 22 μ (0·021 by 0·022 mm.), the largest 126 by 129 μ (0·126 by 0·129 mm).

Their shape is very various, some being spherical, others oval or egg-shaped; the largest examples are oval and slightly compressed. This latter condition is ascertained in vertical sections through the glands when the lining epithelial cells and their nucleus present themselves in profile view.

The intranuclear network[1] contains fibrils of various thickness, either uniform or possessed of irregular thickenings, and larger or smaller trabeculæ. Different parts of one and the same nucleus vary greatly in this respect. The intranuclear network presents itself in its best form in the perfectly fresh and living nuclei, that is, in nuclei that on the warm stage (in blood or humor aqueous) show the amœboid movement. Treated with reagents, the network is less distinct. Sections obtained of tail hardened with chromic acid or picric acid, or a mixture of picric acid and osmic acid, and subsequently stained in carmine or hæmatoxylin, show in some of the nuclei a distinct network, in others it is not so easily perceived; but even in the best examples the network is incomparably less perfect and clear than in the fresh state under the above conditions.

The arrangement of the network varies very much; it is either a more or less uniform reticulum, or the fibres of the peripheral part of the network are arranged in a transverse manner, so as to give it the appearance of a "basket," or its fibrils and trabeculæ are more or less radiating towards a central point or central line. Of great interest are those forms which consist of two nuclei joined by a broader or narrower neck through which the fibrils of the network of one pass into that of the other.

When the gland cells possess two nuclei these are either completely separated or in the state just mentioned. The nuclei with this latter quality are generally the smaller examples. Some of the giant nuclei, both the smallest as well as the largest, in fresh as well as in hardened specimens, are possessed of several larger or smaller knob-like projections, whereby the outline becomes notched and the nucleus looks as if lobed.

In figures 2, 3, 4, 5, 6, and 7 I have represented several of

[1] I purposely avoid the expression "framework" (gerüste) used by Flemming, but use the term (intranuclear) network; the former is bad, for the simple reason that the network is the chief and living part of the nucleus; the term "framework" (gerüste) implies a passive stroma.

the more characteristic forms of these giant nuclei examined in the perfectly fresh state on the warm stage. Those in figs. 2, 3, and 6 show the basket-shaped arrangement of the intranuclear network. Figs. 4 and 7 are probably dividing forms. Fig. 7 had been observed on the warm stage, and it showed slight amœboid movements.

The large thickenings, nucleoli, in figs. 2 and 3 contain vacuoles just like some of the broader trabeculæ of the network.

The interstitial or interfibrillar substance of the intranuclear network is, in the fresh state, quite homogeneous, but not fluid, as can be readily ascertained by applying pressure to the preparation. The limiting membrane becomes then indistinct, and the nucleus, as a whole, greatly flattened; the parts of the reticulum are then seen embedded in a distinct homogeneous matrix, the refractive power of which is higher than the fluid menstruum, but lower than the reticulum. After hardening bits of tail in chromic acid ($\frac{1}{6}$ per cent.) or picric acid (two or three parts of saturated solution of picric acid and one of water) and staining the sections in carmine or hæmatoxylin, the interstitial substance appears slightly stained in some, more deeply in others. In the first instance, the intranuclear network appears in all its delicate details; in the latter, it is difficult to ascertain the fibrils of the network, and sometimes it even looks as if it were altogether absent, the whole nucleus being composed of a uniformly and deeply stained interstitial substance.

If bits of tail be treated with osmic acid (especially in the shape of a mixture with picric acid), and the sections be stained in hæmatoxylin, the interstitial substance appears uniformly and finely granular, and hence greatly interferes with the distinctness of the network.

The epithelial cells lining, or, rather, filling the large saccular or tubular glands situated in the tissue of the tail and opening by means of a very narrow canal through the epidermis on the free surface, are of a very huge size, and of a nature different from what they have been represented by Leydig ('Archiv f. mikr. Anat.,' Band. xii., p. 210). This observer describes them (of *Coecilia* and *Salamandra maculosa*) as composed of (*a*) the cell proper, viz. a protoplasmic portion containing the nucleus, and (*b*) a frothy excretion attached to the former; the cell proper is placed against the membrana propria of the gland sac, whereas the latter is directed towards the duct.

I find the cells filling the gland-sacs in the tail of newt considerably differing from this description. In some glands

the outlines of the individual cells cannot be distinguished; in others they appear of the nature as represented in fig. 1 of Plate XVIII, viz. of various sizes; their shape is either cylindrical or, more commonly, truncated and conical, with their base situated on the membrana propria. Some appear uniform, others consist of (*a*) a transparent, apparently finely granular substance, forming about one half of the cell in a longitudinal direction; (*b*) the other half is less transparent, being filled with coarse, highly refractive particles. In sections of hardened specimens (especially picric acid specimens) stained with hæmatoxylin or carmine the former is seen to be an exceedingly dense network of very minute fibrils,[1] whereas the latter contains, in the meshes of a network of curved and twisted fibrils, real granules and particles of various sizes. The nucleus is situated in many instances in the transparent part, but next the membrana propria; in others it lies partly in the transparent, partly in the granular portion, and in still others it belongs almost entirely to the latter. See fig. 1, Plate XVIII.

Other cells, especially those near the duct, *i. e.* the fine canal passing through the epidermis and formed by a single layer of flattened nucleated cells, are almost completely filled with spherical or elliptical or discoid globules of a

[1] Speaking of the epithelial cells lining the glands of the cloaca of Triton, Leydig (l.c., p. 213) says, "They possess a vacuolated frothy aspect. After reagents and using high powers, it can be ascertained that this is due to a trellis- or network permeating the interior of the cell, that it originates from the protoplasma surrounding the nucleus, and that the larger trabeculæ start as it were in a radial direction from the nucleus while the finer ones lie in the periphery of the cell-wall." . . .

"This peculiar structure of the cell may be placed side by side with what I communicated ten years ago of certain large nuclei of the same animal." . . . . "Ten years ago" would correspond to the year 1865—the above article having been evidently written in 1875—and the communication was made in 'Vom Bau d. Thierischen Körpers,' a work which I regret not to be able to procure.

Leydig continues: "And I may expressly mention that this structure of the cell may have a much greater distribution; at any rate, I am able to see precisely the same structure in the coloured blood-corpuscles of the same amphibian species after acting upon them with Müller's fluid; also here a fine trelliswork passes radially from the nucleus to the periphery of the cell, and at first sight presents itself as 'granulation.'" It appears from this that Leydig was the first to recognise the reticular structure of protoplasm and of the substance of coloured blood-corpuscles, having mentioned it already in 1865, before Frommann 1867 and Heitzmann 1873.

It is, however, important to add that Leydig, as appears further on (l. c., p. 227), regards this reticular structure merely as "a certain transformation of the protoplasm in consequence of the appearance of numerous cavities." The trabecular or spongy matter represents "remains of the original protoplasm attached to the cell-membrane."

fatty nature. In the fresh state they correspond in appearance to fat-globules, and when treated with alcohol and chloroform are, except a limiting outline, entirely dissolved. Hence, in sections treated with alcohol and oil of cloves, these cells appear filled with perfectly transparent, well-defined circles closely pressed against one another (see fig. 1, Plate XVIII). These are the cells which in the fresh state (on the warm stage) while moving are capable of ejecting the fat-globules, as stated above. It thus becomes intelligible how also in the living animal these cells, being situated nearest to the duct, are capable of at once ejecting on to the surface of the skin their fatty secretion. And indeed we find in sections many ducts filled with the same fatty matter. The question arises whether this ejection of the fat-globules represents the sole manner of "secretion," or whether this process (viz. "secretion") is associated, as in the sebaceous glands of mammals, with the expulsion of fat-globules and the cell itself.

I am inclined to think that both are possible; under quiet, normal conditions, I presume secretion is carried out by the cells next the duct ejecting their contents. Under violent struggles, however, when all the muscles of the tail are in very active contraction, the continuous beautiful coat of unstriped muscle fibres—seen by Eberth in frogs, and especially by Leydig in the glands of the cloaca of salamandrinæ as surrounding the gland-sac—by its contraction will be capable of effecting a discharge of the cells themselves next the duct. If a piece of tail (while living) be thrown into a hardening fluid it is for some time actively moving, and the surface of the epidermis becomes covered with minute white spots. Sections prove that these are discharged gland-cells and their secretions lying at the mouth of the ducts.

The facts that all cells lining these saccular glands show amœboid movement on the warm stage, further, the unequal size of these cells (some are many times bigger than others), and some of them containing two nuclei, indicate that reproduction is going on amongst them, in order that those that become lost may be replaced by others.

Leydig states (l. c., p. 138) that the epidermis of all amphibian animals, like that of all other vertebrates, consists of a stratum corneum and rete mucosum.

A section through the skin (of the tail) of newt (*Triton cristatus*) shows that this is not the case, inasmuch as the epidermis does not contain anything of a stratum corneum, as generally understood, and also by Leydig. In a trans-

verse section through tail of newt we notice that the epidermis, whose thickness amounts to 0·081 to 0·094 mm., shows a deep stratum consisting of one or two layers of cells elongated vertically to the surface, their nucleus is generally oval; then follow two to three layers of polyhedral cells, their nucleus is generally round, in some instances oval in a horizontal direction; and, finally, one or two layers of flat cells, their nucleus being flattened horizontally and deeply stained in hæmatoxylin. The top layer is always very highly refractive, and as such differs in a conspicuous manner from the transparent layers underneath. Some preparations show in some places two such layers of highly refractive cell plates, in others only one, and still in others we see one such layer in the act of detaching itself from the layer underneath. The outlines of the cells, especially those of the middle strata are striated, numerous fine fibrils passing from the substance of one cell into that of its neighbours, prickle cells. In preparations obtained from bits of tail hardened in a $\frac{1}{6}$ per cent. solution of chromic acid, these connecting fibrils are in many places of excessive length, the cells, probably through shrinking, having become separated from each other to a much greater extent than is ordinarily seen. And here these fibrils are distinctly seen to pass directly from the reticulated substance of one cell into that of its neighbours, as I described and figured it of the cells of stratified epithelium in a paper in the April number of this journal.

Passingly I may mention the numerous migratory cells, with their folded and constricted nuclei, sometimes drawn out in fine filaments; further, the branched connective-tissue cells with an oblong nucleus, and containing occasionally pigment granules, all these structures being found in the intercellular cement substance of the epidermis.

The variability of the highly refractive top layer of cells, viz., whether one or two, finds its ready explanation in the fact easily noticed on observing newts (kept in water) for several days, viz. that the cuticle is shed in form of a thin transparent membrane. By keeping several animals in one vessel it is difficult to exactly estimate the rapidity and extent of this process of shedding, but if each animal be kept isolated, it can be observed much easier.

The following table shows the exact rapidity with which four adult newts shed their cuticle while observed during May and beginning of June, the animals being kept separately in clear water:—

Female, No. 1 . .	May 1 .	7 .	13 .	19 .	23 .	27 .	June 2.
Female, No. 2 . .	May 21 .	25 .	31 .	June	6 .	12.	
Male, No. 1 . .	May 2 .	9 .	14 .	20 .	25 .	29 .	June 3.
Male, No. 2 .	May 21 .	25 .	June 1 .	8 .	12.		

The figures indicate the day when the cuticle is raised as a thin transparent film over the whole body of the animal; a slight touch brings it down in large flakes, but with a little care it can be removed as a whole, that of the tail and toes included. The first appearance of the shedding in the above animals is noticed already after two or three days, the glistening surface of the body becoming more or less distinctly cloudy. This gradually increases, and after a day or two we notice a thin, transparent membrane becoming raised over the head, dorsum, and abdomen, when viewed in profile in transmitted light. This rapidly increases, and we soon see the whole animal enveloped as it were in a bag formed by that thin membrane, and raised above the surface of the animal to a different extent in different parts. Thus, it is mostly raised on the head and extends gradually hence towards the posterior extremities. The "bag" is open corresponding to the oral cleft, and probably the water getting in at this opening gradually raises mechanically the bag from the surface of the animal while this is swimming about, head, of course, foremost.

The cuticle, when shed, preserves the character of the surface of the different parts of the body, the part derived from the dorsum showing the uniform impressions of the "warts," that from the abdomen showing a transverse arrangement of these impresssions, that from the tail and head being more or less smooth.

The cuticle either shed or removed by means of a forceps can be at once placed into hæmotoxylin, and after staining it—which it does readily—can be floated, as small segments, on to a glass slide and mounted in glycerine.[1]

Under the microscope the cuticle presents itself as a single layer of beautiful transparent squamous polygonal epithelial cells, each with an oval, or sometimes round, nucleus that takes the staining very well. Some cells—not many—possess two nuclei. According to the nature of the surface of the part of the body from which the cuticle is derived, viz. whether smooth or with warts, we notice its surface either smooth, or groups of cells are raised into a smaller or larger convexity.

[1] The cuticle of newt thus stained is a material well suited for class purposes, as it gives an abundance of permanent specimens of continuous masses of beautiful squamous epithelial cells.

The thickness of the cells is about 0·004 mm., the breadth about 0·03 to 0·04 mm.

The cell-substance is generally not deeply stained, and contains few pigment granules around the nucleus.

As a rule, the cells forming the convex sections, *i.e.* corresponding to the surface of the warts, are deeper stained than those between; the cells of the cuticle corresponding to the front part of the head are also, as a rule, more deeply stained than those of the neck. Some of the cells contain one or more larger or smaller holes (vacuoles), probably signs of degeneration; they were noticed in the superficial cells of other amphibia by F. E. Schultze and Eberth. The cells are separated by a very well marked, highly refractive linear interstitial substance, either straight or more or less curved and sinuous. The cells possessing a certain thickness, and their lateral margins not forming quite a vertical plan, but are more or less slanting one way or the other, it follows that when looking at the cuticle from the surface we see that the separating lines, viz. those marking the margins of the individual cells of one surface do not coincide with those of the other. In connection with this cuticle we notice numerous short tubes, some thin, others broad, opening with a small mouth between the cells. Their length is about 0·04 mm., and their breadth is about 0·018 or 0·027, according to whether they belong to the narrow or broad variety. These tubes are made up of a transparent membrane finely and indistinctly longitudinally striated, and showing a compressed nucleus at or about the opening. These structures represent, therefore, one or two flattened cells rolled into a tube. In some instances I can recognise the linear suture. I need hardly add that these tubes are the ducts, or part of them, of the numerous glands of the skin, shed simultaneously with the cuticle. The length of these tubes being less than half the thickness of the whole epidermis, even of hardened specimens, it follows that part only of the glandular ducts is shed with the superficial layer of the epidermis.

In connection with these ducts there may be seen occasionally one, two, or three surrounding epithelial cells removed from the subjacent layer of the epidermis. There can be, therefore, no doubt that the most superficial layer of the epidermis, whether still belonging to this latter or already separated, is composed of nucleated squamous epithelial cells, not of non-nucleated horny "cuticular excretions," as maintained by Leydig (l. c.) for all amphibia.

Seeing then that there exists in the adult newt a conti-

nuous and rapid shedding of the superficial layer of the cells of the epidermis, it naturally follows that a corresponding continuous and rapid new formation of epithelial cells takes place, and accordingly I investigated the epidermis in sections, in order to find, as I expected to find, signs of division of cells and their nuclei. The adult newt being an animal easily procured during the greater part of the year, and its elements being considerably larger than most other vertebrates, easily accessible, would, therefore, be a good object for studying those exceedingly interesting phenomena accompanying the division of nuclei, as first described by Strasburger, Bütschli, Mayzel, Eberth, Hertwig, Auerbach, Balfour, and especially very recently in the beautiful observations of Flemming, Schleicher, and Peremeschko. My expectations were fully realised by the examination of the epidermis of the adult newt, and I will here describe the appearances presented by the dividing nuclei of the epidermis very briefly, since my observations in many respects fully coincide with those of Flemming and Peremeschko, observed by the former in *Salamandra maculosa* and its embryo, by the latter in the embryo of *Triton cristatus*. Following the plan of Flemming ('Archiv f. mikro Anat.,' Bnd. xvi, p. 363), I hardened my object in picric acid or chromic acid and stained it afterwards in hæmatoxylin, and I found it very good for the demonstration of the different forms of dividing nuclei. The picric acid I used is a mixture of two or three parts of a saturated solution and one part of water, the chromic acid is a $\frac{1}{6}$ per cent. solution. Bits of tail —about $\frac{1}{4}$ or $\frac{1}{3}$ inch long—are placed in either of these fluids and kept there for seven to ten days, they are then placed for a short time ($\frac{1}{4}$ or $\frac{1}{2}$ hour) in spirit, embedded and used for cutting fine vertical sections. These are thoroughly washed in water, stained in very dilute hæmatoxylin and then prepared in the ordinary way for mounting and preserving in solution of Canada balsam. The sections prepared in picric acid are preferable to those in chromic acid, although the latter have many good points about them.

The phenomena of division of nuclei to be observed in these specimens are confirmatory of the statements made by Flemming in his very exhaustive article, in which he minutely describes the different changes the intranuclear network undergoes during division, as observed by him in the living state and after reagents. In the same paper Flemming gives an exhaustive and critical review of the observations and assertions on the same subject by his pre-

decessors, and I can therefore omit detailed references to other observers.

We notice in such a section that the nuclei of the two deeper layers of cells are oval, and placed vertically to the surface; they possess a sharp limiting membrane, and contain a uniform reticulum, intranuclear network, varying between the reticulum of minute fibrils to that of a spongy honeycombed structure. The interstitial substance of this reticulum is homogeneous and transparent in logwood. There is no trace of any nucleolus. Division of nuclei being limited to these two layers, we are justified in considering them as in a ripe state, and we have, therefore, here much additional evidence that the nucleolus is not a necessary feature in the structure of a nucleus, and that it is altogether absent in nuclei, that may be regarded as ripe and fully formed (see figs. 8 and 9, Plate XVIII). The nuclei of the middle strata of the epidermis show a more or less distinct reticulum, and in it larger or smaller accumulations—nucleoli; the interstitial substance is homogeneous, but in many cases more or less stained in hæmatoxylin.

In all cases, however, we find the small, bright dots included in the network; these, as stated by me on so many occasions, are fibrils of the reticulum viewed in optical section.

Amongst the nuclei of the two deep layers of cells we notice some that are somewhat larger than the rest, and contain very beautiful, deeply stained fibrils, either twisted and coiled into a more or less dense convolution (Flemming), or arranged like a basket (Eberth), viz. most fibrils are peripheral, and have a transverse direction; hence, the surface of the nucleus in the latter case shows a transverse striation. But in both instances, viz. the "convolution" and the "basket," the fibrils are connected into a network (see figs. 10—13, Pl. XVIII). The membrane of the nuclei showing this arrangement is less marked than in the other nuclei of the ordinary kind, appearing not as a continuous structure, but more or less due to the close position of the fibrils.

These forms are regarded by Flemming as the initial stages of the coming division of the nucleus. I do not find anything that would be contrary to such an explanation. Like Flemming, I find all forms intermediary between the ordinary nucleus as above described and the enlarged nuclei with "convolutions" or basket-shaped arrangement of the intranuclear network.

In some cases the "convolutions" are very dense, and

hence many of the fibrils are seen endwise as bright dots or "granules." This appearance is incorrectly interpreted by Mayzel, Eberth, and especially Schleicher and Peremeschko, who describe the nuclei as at first containing "granules," which gradually arrange themselves into fibrils. I am at one with Flemming in opposing such an interpretation, since I maintain, with him, that before the fibrils arrange themselves into "convolution" and "basket," there is already a well-formed reticulum in the nucleus.

Nuclei of this kind can be seen in the deepest and in the next following layer.

Then we find nuclei somewhat larger, but without any limiting membrane whatever; they may be described with Flemming as containing deeply-stained filaments arranged in the shape of a "rosette" or "wreath;" the filaments are in different examples of different thickness; they form a loop at the periphery, and approach each other in the centre (see figs. 14, 17 and 18). Between the nuclei with "convolutions" or "basket"-shaped arrangement of filaments, and those in which the latter form a "rosette" or "wreath," we find many intermediary forms. See also Flemming, l. c., p. 376, and the beautiful figures on Plate XVII, accompanying his paper.

Further, we pass from these to large nuclei, also without any membrane, in which the deeply-stained fibrils are arranged like a single aster ("Monaster"), apparently terminating freely at the periphery, but connected into a central network. Mr. Balfour has also described and figured this form as the "stellate variety" of dividing nuclei of the developing ova of the embryo (this Journal, No. lxxii, p. 395). Like Flemming, I also find the fibrils of this form, as a rule, much thicker than in any of the preceding ones (see fig. 19).

Next, we trace these into nuclei without a membrane, in which the fibrils are similar in appearance to the preceding ones, but arranged as a double aster "(Dyaster)" (see figs. 20, 21, 22).

The majority of the forms described as "rosette" or "wreath," and as "monaster" and "dyaster," are found amongst the deepest layer, but occasionally we meet one or the other of them in the next following, or even the further layer; they are all very conspicuous on account of their size, and owing to this the cell itself is very much bulged out laterally.

In the "dyaster," that I find in my specimens, the fibrils of one aster are connected with those of the other. The

dyaster represents a more or less elliptical body, at the poles of which the fibrils are connected into a network; they pass from one pole to the other as isolated longitudinal fibrils. We have a form that coincides with the spindle of Strasburger, but in which the fibrils form a network at the poles. Flemming has figured them very beautifully on his Plates XVI and XVII.

The axis, *i. e.* the line joining the poles of any "dyaster," lies in most instances parallel with the surface of the epidermis, and only in few instances have I seen it more or less vertical. This is, in so far, of interest, as it proves that in many instances the two daughter nuclei (derived from the division of the dyaster), and, consequently, also, the two daughter cells, do not lie above one another in a line vertical to the surface of the epidermis, but side by side.

Then we find that the dyaster divides into two small separate monasters, the longitudinal fibrils running from one pole to the other of the dyaster dividing in the middle one by one. We have finally two small nuclei side by side, but separate, the fibrils of each possessing the arrangement of a monaster.

I find, just like Flemming, who so exhaustively described them, that these daughter nuclei undergo the same changes as the mother nuclei did, but in a reverse order, viz. passing from the state of monaster into that of a "rosette" or "wreath," from this into that of a "basket" or "convolution," and, finally, into a nucleus containing a uniform spongy reticulum. While the daughter nuclei undergo these changes, except the last, they are easily distinguishable from similar forms of mother nuclei, owing to the smallness of the former and their positions in couples (see figs. 22—25, Pl. XVIII).

Just as is the case with mother nuclei in the stages of rosette, wreath, and monaster, so also the daughter nuclei of the analogous forms do not possess any membrane; in the "convolution" and "basket" of daughter nuclei the membrane is very indistinct, and is also here due to the close position of the fibrils.

As has been mentioned above, the majority of daughter nuclei lie at first side by side, *i. e.* in an axis parallel to the surface. But after the cell substance itself has become divided, the daughter nuclei gradually change their relative position, the (imaginary) axis joining them, rotating so as to assume a position vertical to the surface of the epidermis.

The daughter nuclei enclosed in a still undivided

generally belong to the deepest layer, but they soon become shifted into the next following stratum.

A point of great importance is the relation of the fibrils of the nucleus in the different stages of division to the cell substance itself. I have on two occasions (this Journal, July, 1878, and April, 1879) referred to a connection of the fibrils of the intranuclear network with the reticulum representing the protoplasm of the cell, and on carefully examining my specimens of dividing nuclei I find that also the fibrils of these are intimately connected with the cell substance. The forms mentioned as rosette or wreath, but especially as monaster, are those in which—the examination being greatly facilitated by the absence of any membrane—in many instances I can most positively see a direct connection between the fibrils of the nucleus and the reticulum representing the cell substance. Such a connection will be found represented in figs. 14—19 of Plate XVIII. It is true the observation requires very favorable conditions, viz. the nucleus must be a large one, must be seen on its broad surface, the light must be good, the sections thin, and the power high. Zeiss's new oil immersion, $\frac{1}{12}$ and $\frac{1}{18}$[1] inch, have proved here invaluable.

The fibrils of the nucleus taking the staining very deeply seem at first altogether distinct from the surrounding cell substance, which is either not at all or only slightly stained, but nevertheless, on careful inspection, it will be found that the fibrils, especially of the monaster, although they appear to terminate singly in the periphery and with a blunt extremity, do not so terminate but pass on, unstained, into the reticulum of the cell substance. The difference of the fibrils of the nucleus and the cell substance in their staining power is no doubt due to an essential chemical distinction, but this does not necessarily imply that the two substances cannot form an anatomical continuity. Nor, it seems to me, does the observation by Schleicher ('Archiv f. mikr. Anat.,' Bd. xvi., p. 261) of the peculiar state of contractility—"karyokinesis"—of the nucleus of cartilage cells preceding division, nor that by Peremeschko of similar appearances in the dividing nucleus of epithelial cells of embryo Triton, make such a connection between cell substance and nucleus improbable.

By the observations of Stricker ('Sitzungsber. d. k. Akad. d. Wiss.,' Vienna, June, 1877) it is established that the nucleus of some colourless blood-corpuscles possesses contractility while within the cell as well as after separation

[1] These two lenses, although of very great magnifying power, are nevertheless marvellous in sharp definition.

from it, and it is likewise established by Stricker, that the nucleus of those cells is during life in direct anatomical continuity with the cell substance, and further that by the appearance of a membrane a central portion of the cell substance becomes temporarily differentiated as nucleus. I have also mentioned on a former page that the giant nuclei of the gland cells of newt show local contractions of their reticulum. The connection of the fibrils of the dividing nucleus with the cell substance and the contractility of both, seems to me to explain also the peculiar appearances described by Auerbach as "karyolitic figure" and observed by many others (Flemming, Fol, Bütschli, Strasburger, O. Hertwig, and others) in dividing nuclei of ovum and other cells, viz. a radiar arrangement of fibrils of what corresponds to the cell substance towards the nucleus, when single as well as after division—in the former case as a single, in the latter as a double "karyolytic figure." We have to assume that, owing probably to contraction of the intranuclear network, the fibrils of the intracellular reticulum are drawn towards the former. Whether at the same time an exchange of the two substances takes place, or whether the nucleus alone takes in matter from the cell, it is difficult to decide; both seem probable from theoretical considerations so thoroughly discussed by Auerbach, Strasburger, Bütschli, Flemming, and Schleicher.

A point not less interesting is the question, whether the division of the nucleus takes place in all cells of the epidermis of adult newt after the same complicated manner as described in the preceding, or whether there is in addition another simpler mode, so often mentioned in normal and pathological histology as that of simple cleavage. Flemming proposes the term "indirect" multiplication of the nucleus for the former complex mode, and "direct" for the latter simple mode, and we shall accept these terms in the following description.

Auerbach and Eberth accept such a direct mode of division, Flemming questions it, although he does not think it quite impossible. This last named author describes forms of nuclei which might be taken as indicative of simple cleavage, viz. ordinary nuclei kidney-shaped and lobed, or beset with more or less deep constrictions; but he finds reasons to believe that these are only temporary appearances due probably to movement.

As I mentioned on a former page the very rapid shedding of the superficial layer of the cells of the epidermis

me to examine the epidermis with reference to the process of division, and we have seen that division of nuclei occurs merely in the deepest or the next following layer. Considering that the superficial layer of cells is shed within five or six days (see the tables on a previous page), we should be justified in expecting to find very abundant division amongst the nuclei of the deeper layer. This, however, is not the case by any means. True, some of the stages of indirect division described on a former page are, according to Flemming and Peremeschko's direct observations, only of very short duration, but I think I can show that all forms of nuclei indicating such divisions—from that of the "convolution" of the mother nucleus to the "convolution" of the daughter nucleus—do not represent but a relatively small contingent, not sufficient to account for the copious new-formation of nuclei and cells that must be going on in order to defray such a loss of cells and nuclei as is represented by the shedding of the cuticle within five or six days. I have counted in several fields in a preparation prepared with picric acid and stained with logwood, all the forms of nuclei indicating indirect division, and I found the following:

The preparation is a vertical section through the tail of a female adult newt; the thickness of the section is such that the cells of the epidermis lie two deep. The counting was made with the objective E of Zeiss. The size of the field of the microscope under this lens on my stand comprises about 30 nuclei of the deepest layer of cells, *i. e.* the layer next the corium, and as the section is two cells deep, it follows that we may take 60 nuclei as comprised in the deepest layer of one field. Of course this figure 60 is only approximately correct, since the section is not everywhere of equal thickness, and since the nuclei are not everywhere placed equally closely. But I should think the error in accepting that figure cannot be great. As I do not claim any degree of accuracy, we may accept that number as sufficiently serviceable.

In Field 1, I count one "wreath;" one divided, each daughter nucleus "monaster;" one "basket."
In Field 2, three "convolutions;" one divided, each daughter nucleus "basket."
In Field 3, one "wreath;" one "convolution."
In Field 4, one "convolution;" two "baskets;" one divided, each daughter nucleus "basket."
In Field 5, two "convolutions."
In Field 6, one divided, each daughter nucleus "basket."
In Field 7, one "dyaster."

All these "fields" follow each other consecutively, so that we may say that amongst about 840 nuclei (that is, counting the nuclei of the two lowest layers, each of these two deep), we find 17 only, indicative of indirect division.

In another specimen (of the same tail), prepared in exactly the same manner, we find:

In Field 1, two "wreaths;" two "monasters;" five "convolutions;" two "baskets."

In Field 2, two divided, each daughter nucleus "convolution;" one "monaster;" one divided, each daughter nucleus "basket;" two "wreaths;" three "convolutions;" three "baskets."

Thus, in these two fields, corresponding, therefore, to about 240 nuclei we find 23 forms indicative of indirect division. In connection with this I have to add that I have taken great care not to omit any of those forms; this is to a certain extent facilitated by the conspicuous appearance presented by the nuclei of this kind.

As I do not know at what rate the division of the nuclei takes place, and as the thickness of the epidermis is not constant in all places, I am not able to use in any, but a very approximate manner, the above numbers, and such as they are, they seem to me, on account of their smallness, to indicate that there must be another method of reproduction of nuclei in addition to the indirect one. And we have only to examine carefully the deeper strata of the epidermis to convince ourselves of the presence of nuclei which appear to be in different stages of cleavage. They are oval nuclei, differing as regards their membrane and honeycomb reticulum in no way from the other nuclei of these layers. I have represented in figures 26—32, Pl. XVIII, the most characteristic forms of nuclei in the various stages of cleavage. They vary in numbers in different parts of a section, and appear to me to be more than merely constricted or lobed shapes, such as described by Flemming as being of a temporary nature. Figures 29, 30, and 31 seem to me quite convincing.

I may state here that I have found very numerous nuclei, in the various stages of cleavage, also in the epithelium lining the neck of the duct of the cutaneous glands.

It is quite possible that the nuclei undergoing the indirect division in the adult have inherited the power to do this from the ovum, the nuclei of which, as is now well known from numerous observations on different vertebrate and invertebrate animals, undergo the indirect mode of divisi[illegible]. It is probable, from Peremeschko's observations, that

embryo Triton the nuclei of all, or nearly all, epithelial cells undergo the indirect division; but since it is equally probable that in the adult only a relatively small number of nuclei possesses this property, it follows that many of them lose this power and degenerate in the manner of division, becoming degraded into nuclei that multiply after the more plebeic manner of simple cleavage. By doing this, nature evidently gains her end under great saving of energy, since the existence of these nuclei is only of short duration.

As supporting the assumption that nuclei divide after the "direct" manner, viz. by cleavage, may be regarded those nuclei in which the fibrils have arranged themselves, as if those nuclei were going to divide in the indirect way, but for some reason or other did not succeed in doing so, but divided ultimately by cleavage. I refer to figs. 33, 34, and 35, which I have selected as the more characteristic forms; fig. 33 represents a "convolution," 34 and 35 "baskets" all undergoing the "direct" mode of division.

A good object for demonstrating the different forms of nuclei while undergoing the indirect mode of division is the bladder of adult frog prepared with chloride of gold. The organ is filled *in situ* with chloride of gold ($\frac{1}{3}$ per cent.) until it is well distended; it is then ligatured at the neck, and placed in chloride of gold for about half an hour, then opened and exposed to the light in slightly acidulated water. Examining the inner surface of a small portion spread out on a slide and mounted in glycerin, we meet with many beautiful forms of "convolutions," "monasters," "wreaths," "dyasters," and couples of small daughter nuclei. The tail of tadpole prepared in chloride of gold (see 'Handbook for the Physiolog. Laboratory,' p. 41) shows also, amongst the epithelium of both surfaces, forms of dividing nuclei, especially "baskets," "monasters," and "dyasters." Their number, however, is relatively small. The great majority of the nuclei present a uniform network of fibrils or rods. The nuclei of the epithelium of the bladder of frog are preferable to those of the tail of the tadpole, being of a much larger size.

P. S.—Since the printing of the foregoing I have received from my friend Professor Flemming, in Kiel, two of his preparations of embryo Salamander, and I see in them the most exquisite forms of nuclei dividing after the indirect mode, as figured by F. in his paper.

On the Early Development *of the* Lacertilia, *together with some* Observations *on the* Nature *and* Relations *of the* Primitive Streak.

By F. M. Balfour, M.A., F.R.S., Fellow of Trinity College, Cambridge. (With Plate XIX.)

Till quite recently no observations were recorded on the early developmental changes of the reptilian ovum. Not long ago Professors Kupffer and Benecke published a preliminary note on the early development of *Lacerta agilis* and *Emys Europea*.[1] I have myself also been able to make some observations on the embryo of *Lacerta muralis*. The number of my embryos has been somewhat limited, and most of those which I have had have been preserved in bichromate of potash, which has turned out a far from satisfactory hardening reagent. In spite of these difficulties I have been led on some points to very different results from those of the German investigators, and to results which are more in accordance with what we know of other Sauropsidan types. I commence with a short account of the results of Kupffer and Benecke.

Segmentation takes place exactly as in birds, and the resulting blastoderm, which is thickened at its edge, spreads rapidly over the yolk. Shortly before the yolk is half enclosed a small embryonic shield (area pellucida) makes its appearance in the centre of the blastoderm, which has, in the meantime, become divided into two layers. The upper of these is the epiblast, and the lower the hypoblast. The embryonic shield is mainly distinguished from the remainder of the blastoderm by the more columnar character of its constituent epiblast cells. It is somewhat pyriform in shape, the narrower end corresponding with the future posterior end of the embryo. At the narrow end an invagination takes place, which gives rise to an open sac, the blind end of which is directed forwards. The opening of this sac is regarded by the authors as the blastopore. A linear thickening of epiblast arises in front of the blastopore, along the median line of which the medullary groove soon appears. In the caudal region the medullary folds spread out and enclose between them the blastopore, behind which they soon meet again. On the conversion of the medullary groove into a closed canal the blastopore becomes obliterated. The mesoblast grows out from the lip of the blastopore as four masses. Two of these are lateral: a third is anterior and median, and, although at first independent of the epiblast, soon attaches itself to it, and forms with it a kind of

[1] 'Die Erste Entwicklungsvorgänge am Ei der Reptilien,' Königsberg, 1878.

axis-cord. A fourth mass applied itself to the walls of
formed by invagination.

With reference to the very first developmental phenom
observations are confined to two stages during the segmen
In the earliest of these the segmentation was about half con
in the later one it was nearly over. My observations
stages bear out generally the statements of Kupffer and B
In the second of them the blastoderm was already imp
divided into two layers—a superficial epiblastic layer forn
single row of cells, and a layer below this several row
Below this layer fresh segments were obviously being a
the blastoderm from the subjacent yolk.

Between the second of these blastoderms and my nex
there is a considerable gap. The medullary plate
established, and is marked by a shallow groove which
deeper in front. A section through the embryo is repr
in Pl. XIX, Series A, fig. 1. In this figure there
seen the thickened medullary plate with a shallow me
groove, below which are two independent plates of m
(*me. p.*), one on each side of the middle line, very imp
divided into somatopleuric and splanchnopleuric layers.
the mesoblast is a continuous layer of hypoblast (*hy.*),
develops a rod-like thickening along the axial line (*ch.*).
rod becomes in the next stage the notochord. Althou
embryo is not well preserved I feel very confident in assert
continuity of the notochord with the hypoblast at this sta

At the hind end of the embryo is placed a thickened r
tissue which continues the embryonic axis. In this ridge
layers coalesce, *and I therefore take it to be equivalent
primitive streak of the avian blastoderm.* It is son
triangular in shape, with the apex directed backward, the
base placed in front.

At the junction between the primitive streak and the b
derm is situated a passage, open at both extremities, le
from the upper surface of the blastoderm obliquely forwar
the lower.

The dorsal and anterior wall of this passage is formed
distinct epithelial layer, continuous at its upper extremity
the epiblast, and at its lower with the notochordal plate, so
it forms a layer of cells connecting together the epiblast and h
blast. The hinder and lower wall of the passage is formed b
cells of the primitive streak, which only assume a columnar
near the dorsal opening of the passage (*vide* fig. 4). This pas
is clearly the blind sac of Kupffer and Benecke, who, if I am

[1] For these two specimens, which were hardened in picric acid, I
debted to Dr. Kleneinberg.

mistaken, have overlooked its lower opening. As I hope to show in the sequel, it is also the equivalent of the neurenteric passage, which connects the neural and alimentary canals in the Icthyopsida, and therefore represents the blastopore of Amphioxus Amphibians, &c.

Series A, figs. 2, 3, 4, 5, illustrate the features of the passage and its relation to the embryo.

Fig. 2 passes through the ventral opening of the passage. The notochordal plate (*ch'.*) is vaulted over the opening, and on the left side is continuous with the mesoblast as well as the hypoblast. Figs 3 and 4 are taken through the middle part of the passage (*ne.*), which is bounded above by a continuation of the notochordal plate, and below by the tissue of the primitive streak. The hypoblast (*hy.*), in the middle line, is imperfectly fused with the mesoblast of the primitive streak, which is now continuous across the middle line. The medullary groove has disappeared, but the medullary plate (*m p.*) is quite distinct.

In fig. 5 is seen the dorsal opening of the passage (*ne.*). If a section behind this had been figured, as is done for the next series (B), it would have passed through the primitive streak, and, as in the chick, all the layers would have been fused together. The epiblast in the primitive streak completely coalesces with the mesoblast; but the hypoblast, though attached to the other layers in the middle line, can always be traced as a distinct stratum.

Fig. B is a surface view of my next oldest embryo. The medullary groove has become much deeper, especially in front. Behind it widens out to form a space equivalent to the sinus rhomboidalis of the embryo bird. The amnion forms a small fold covering over the cephalic extremity of the embryo, which is deeply embedded in the yolk. Some somites (protovertebræ) were probably present, but this could not be made out in the opaque embryo.

The woodcut (fig. 1) represents a diagrammatic longitudinal section through this embryo, and the sections belonging to Series B illustrate the features of the hind end of the embryo and of the primitive streak.

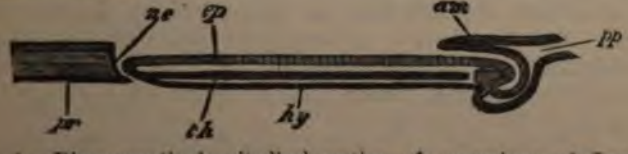


FIG. 1.—Diagrammatic longitudinal section of an embryo of Lacerta. *pp.* Body cavity. *am.* Amnion. *ne.* Neurenteric canal. *ch.* Notochord. *hy.* Hypoblast. *ep.* Epiblast. *pr.* Primitive streak.

As is shown in fig. 1, the notochord (*ch.*) has now throughout the region of the embryo become separated from the subjacent hypoblast, and the lateral plates of mesoblast are distinctly divided into somatic and splanchnic layers. The medullary groove is continued as a deepish groove up to the opening of the neurenteric passage, which thus forms a perforation in the floor of the hinder end of the medullary groove (*vide* Series B, figs. 2, 3, and 4).

The passage itself is somewhat shorter than in the previous stage, and the whole of it is shown in a single section (fig. 4). This section must either have been taken somewhat obliquely, or else the passage have been exceptionally short in this embryo, since in an older embryo it could not all be seen in one section.

The front wall of the passage is continuous with the notochord, which for two sections or so in front remains attached to the hypoblast (figs. 2 and 3). Behind the perforation in the floor of the medullary groove is placed the primitive streak (fig. 5), where all the layers become fused together, as in the earlier stage. Into this part a narrow diverticulum from the end of the medullary groove is continued for a very short distance (*vide* fig. 5, *mc.*).

The general features of the stage will best be understood by an examination of the diagrammatic longitudinal section, represented in woodcut, fig. 1. In front is shown the amnion (*am.*), growing over the head of the embryo. The notochord (*ch.*) is seen as an independent cord for the greater part of the length of the embryo, but falls into the hypoblast shortly in front of the neurenteric passage. The neurenteric passage is shown at *ne.*, and behind it is shown the primitive streak.

In a still older stage, represented in surface view on Pl. XIX, fig. C, medullary folds have nearly met above, but have not yet united. The features of the passage from the neural groove to the hypoblast are precisely the same in the embryo just described, although the lumen of the passage has become somewhat narrower. There is still a short primitive streak behind the embryo.

The neurenteric passage persists but a very short time after the complete closure of the medullary canal. It is in no way connected with the allantois, as conjectured by Kupffer and Benecke, but the allantois is formed, as I have satisfied myself by longitudinal sections of a later stage, in the manner already described by Dobrynin, Gasser, and Kölliker for the bird and mammal.

The general results of Kupffer's and Benecke's observations, with the modifications introduced by my own observations, are as follows:—After the segmentation and the formation of the embryonic shield (area pellucida) the blastoderm becomes dis-

tinctly divided into epiblast and hypoblast.[1] At the hind end of the shield a somewhat triangular primitive streak is formed by the fusion of the epiblast and hypoblast with a number of cells between them, which are probably derived from the lower rows of the segmentation cells. At the front end of the streak a passage arises, open at both extremities, leading obliquely forwards through the epiblast to the space below the hypoblast. The walls of the passage are formed of a layer of columnar cells continuous both with epiblast and hypoblast. In front of the primitive streak the body of the embryo becomes first differentiated by the formation of a medullary plate, and at the same time there grows out from the primitive streak a layer of mesoblast, which spreads out in all directions between the epiblast and hypoblast. In the axis of the embryo the mesoblast plate is stated by Kupffer and Benecke to be continuous across the middle line, but this appears very improbable. In a slightly later stage the medullary plate becomes marked by a shallow groove, and the mesoblast of the embryo is then undoubtedly constituted of two lateral plates, one on each side of the median line. In the median line the notochord arises as a ridge-like thickening of the hypoblast which becomes very soon quite separated from the hypoblast, except at the hind end, where it is continued into the front wall of the neurenteric passage. It is interesting to notice the remarkable relation of the notochord to the walls of the neurenteric passage. More or less similar relations are also well marked in the case of the goose and the fowl (Gasser),[2] and support the conclusion deducible from the lower forms of vertebrata, that the notochord is essentially hypoblastic.

The passage at the front end of the primitive streak forms the posterior boundary of the medullary plate, though the medullary groove is not at first continued back to it. The anterior wall of this passage connects together the medullary plate and the notochordal ridge of the hypoblast. In the succeeding stages the medullary groove becomes continued back to the opening of the passage, which then becomes enclosed in the medullary folds, and forms a true neurenteric passage. It becomes narrowed as the medullary folds finally unite to form the medullary canal, and eventually disappears.

I conclude this paper with a concise statement of what appears to me the probable nature of the much-disputed organ, the primitive streak, and of the arguments in support of my view.

[1] This appears to me to take place before the formation of the embryonic shield.

[2] Gasser, 'Der Primitivstreifen bei Vogelembryonen,' Marburg, 1878.

In a paper on the primitive streak in the 'Quart. Journ. of Mic. Sci.,' in 1873 (p. 280), I made the following statement with reference to this subject:—"It is clear, therefore, that the primitive groove must be the rudiment of some ancestral feature. . . . . It is just possible that it is the last trace of that involution of the epiblast by which the hypoblast is formed in most of the lower animals."

At a later period, in July, 1876, after studying the development of Elasmobranch fishes, I enlarged the hypothesis in a review of the first part of Prof. Kölliker's 'Entwicklungsgeschichte.' The following is the passage in which I speak of it:[1]

"In treating of the exact relation of the primitive groove to the formation of the embryo, Professor Kölliker gives it as his view that though the head of the embryo is formed independently of the primitive groove, and only secondarily unites with this, yet that the remainder of the body is without doubt derived from the primitive groove. With this conclusion we cannot agree, and the very descriptions of Professor Kölliker appear to us to demonstrate the untenable nature of his results. We believe that the front end of the primitive groove at first occupies the position eventually filled by about the third pair of protovertebræ, but that as the protovertebræ are successively formed, and the body of the embryo grows in length, the primitive groove is carried further and further back, so as always to be situated immediately behind the embryo. As Professor Kölliker himself has shown it may still be seen in this position even later than the fortieth hour of incubation.

"Throughout the whole period of its existence it retains a character which at once distinguishes it in sections from the medullary groove.

"Beneath it the epiblast and mesoblast are *always fused*, though they are always separate elsewhere; this fact, which was originally shown by ourselves, has been very clearly brought out by Professor Kölliker's observations.

"The features of the primitive groove which throw special light on its meaning are the following:—

"(1.) It does not enter directly into the formation of the embryo.

"(2.) The epiblast and mesoblast always become fused beneath it.

"(3.) It is situated immediately behind the embryo.

"Professor Kölliker does not enter into any speculations as to the meaning of the primitive groove, but the above-mentioned facts appear to us clearly to prove that the primitive groove is a

[1] 'Journal of Anat. and Phys.,' vol. x, pp. 790 and 791. Compare also my monograph on 'Elasmobranch Fishes,' note on p. 68.

rudimentary structure, the origin of which can only be completely elucidated by a knowledge of the development of the Avian ancestors.

"In comparing the blastoderm of a bird with that of any anamniotic vertebrate, we are met at the threshold of our investigations by a remarkable difference between the two. Whereas in all the lower vertebrates the embryo is situated at the *edge* of the blastoderm, it is in birds and mammals situated in the centre. This difference of position at once suggests the view that the primitive groove may be in some way connected with the change of position in the blastoderm which the ancestors of birds must have undergone. If we carry our investigations amongst the lower vertebrates a little further, we find that the Elasmobranch embryo occupies at first the normal position at the edge of the blastoderm, but that in the course of development the blastoderm grows round the yolk far more slowly in the region of the embryo than elsewhere. Owing to this, the embryo becomes left in a bay, the two sides of which eventually meet and coalesce in a linear fashion immediately behind the embryo, thus removing the embryo from the edge of the blastoderm and forming behind it a linear streak not unlike the primitive streak. We would suggest the hypothesis that the primitive groove is a rudiment which gives the last indication of a change made by the Avian ancestors in their position in the blastoderm, like that made by Elasmobranch embryos when removed from the edge of the blastoderm and placed in a central situation similar to that of the embryo bird. On this hypothesis the situation of the primitive groove immediately behind the embryo, as well as the fact of its not becoming converted into any embryonic organ would be explained. The central groove might probably also be viewed as the groove naturally left between the coalescing edges of the blastoderm.

"Would the fusion of epiblast and mesoblast also receive its explanation on this hypothesis? We are of opinion that it would. At the edge of the blastoderm which represents the blastopore mouth of Amphioxus all the layers become fused together in the anamniotic vertebrates. So that if the primitive groove is in reality a rudiment of the coalesced edges of the blastoderm, we might naturally expect the layers to be fused there, and the difficulty presented by the present condition of the primitive groove would rather be that the hypoblast is not fused with the other layers than that the mesoblast is indissolubly united with the epiblast. The fact that the hypoblast is not fused with the other layers does not appear to us to be fatal to our hypothesis, and in Mammalia, where the primitive and medullary grooves present precisely the same relations as in birds, all three layers are, accord-

ing to Hensen's account, fused together. This, however, is denied by Kölliker, who states that in Mammals, as in Birds, only the epiblast and mesoblast fuse together. Our hypothesis as to the origin of the primitive groove appears to explain in a fairly satisfactory manner all the peculiarities of this very enigmatical organ; it also relieves us from the necessity of accepting Professor Kölliker's explanation of the development of the mesoblast, though it does not, of course, render that explanation in any way untenable."

At a somewhat later period Rauber arrived at a more or less similar conclusion, which, however, he mixes up with a number of opinions from which I am compelled altogether to dissent.[1]

The general correctness of my view, as explained in my second quotation, appears to me completely established by Gasser's beautiful researches on the early development of the chick and goose,[2] and by my own observations just recorded on the lizard. While at the same time the parallel between the blastopore of Elasmobranchii and of the Sauropsida, is rendered more complete by the discovery of the neurenteric passage in the latter group, which was first of all made by Gasser.

The following paragraphs contain a detailed attempt to establish the above view by a careful comparison of the primitive streak and its adjuncts in the amniotic vertebrates with the blastopore in Elasmobranchii.

In Elasmobranchii the blastopore consists of the following parts:—(1), a section at the end of the medullary plate, which becomes converted into the neurenteric canal;[3] (2), a section forming what may be called the yolk blastopore, which eventually constitutes a linear streak connecting the embryo with the edge of the blastoderm (*vide* my monograph on Elasmobranch fishes, pp. 68 and 81). In order to establish my hypothesis on the nature of the primitive streak, it is necessary to find the representatives of both these parts in the primitive streak of the amniotic vertebrates. The first section ought to appear as a passage from the neural to the enteric side of the blastoderm at the posterior end of the medullary plate. At its front edge the epiblast and hypoblast should be continuous, as they are at the hind end of the embryo in Elasmobranchii, and, finally, the passage should, on the closure of the medullary groove, become converted into the *neurenteric canal*. All these conditions are exactly fulfilled by the opening at the front end of

[1] "Primitivrinne u. Urmund," 'Morphologisches Jahrbuch.,' Band ii, p. 551.

[2] Gasser, 'Der Primitivstreifen bei Vogelembryonen,' Marburg, 1878.

[3] I use this term for the canal connecting the neural and alimentary which was first discovered by Kowalevsky.

the primitive streak of the lizard (*vide* woodcut, fig. 1). In the chick there is at first no such opening, but, as I hope to show in a future paper, it is replaced by the epiblast and hypoblast falling into one another at the front end of the primitive streak. At a later period, as has been shown by Gasser,[1] there is a distinct rudiment of the neurenteric canal in the chick, and a complete canal in the goose. Finally, in mammals, as has been shown by Schäfer[2] for the guinea-pig, there is at the front end of the primitive streak a complete continuity between epiblast and hypoblast. The continuity of the epiblast and hypoblast at the hind end of the embryo in the bird and the mammal is a rudiment of the continuity of these layers at the dorsal lip of the blastopore in Elasmobranchii, Amphibia, &c. The second section of the blastopore in Elasmobranchii or yolk blastopore is, I believe, partly represented by the primitive streak. The yolk blastopore in Elasmobranchii is the part of the blastopore belonging to the yolk sac as opposed to that belonging to the embryo, and it is clear that the primitive streak cannot correspond to the whole of this, since the primitive streak is far removed from the edge of the blastoderm long before the yolk is completely enclosed. Leaving this out of consideration the primitive streak, in order that the above comparison may hold good, should satisfy the following conditions:

1. It should connect the embryo with the edge of the blastoderm.

2. It should be constituted as if formed of the fused edges of the blastoderm.

3. The epiblast of it should eventually not form part of the medullary plate of the embryo, but be folded over on to the ventral side.

The first of these conditions is only partially fulfilled, but, considering the rudimentary condition of the whole structure, no great stress can, it seems to me, be laid on this fact.

The second condition seems to me very completely satisfied. Where the two edges of the blastoderm become united we should expect to find a complete fusion of the layers such as takes place in the primitive streak; and the fact that in the primitive streak the hypoblast does not so distinctly coalesce with the mesoblast as the mesoblast with the epiblast cannot be urged as a serious argument against me.

The growth outwards of the mesoblast from the axis of the primitive streak is probably a remnant of the invagination of the

[1] Loc. cit.

[2] "A contribution to the history of the development in the Guinea-pig," 'Journal of Anat. and Phys.,' vol. xi, pp. 332—336.

hypoblast and mesoblast from the lip of the blastopore in Amphibia, &c.

The groove in the primitive streak may with great plausibility be regarded as the indication of a depression which would naturally be found along the line where the thickened edges of the blastoderm became united.

With reference to the third condition, I will make the following observations. The neurenteric canal, as it is placed at the extreme end of the embryo, must necessarily, with reference to the embryo, be the hindermost section of the blastopore, and therefore the part of the blastopore apparently behind this can only be so owing to the embryo not being folded off from the yolk sac; and as the yolk sac is in reality a specialised part of the ventral wall of the body, the yolk blastopore must also be situated on the ventral side of the embryo.

Kölliker and other distinguished embryologists have believed that the epiblast of the whole of the primitive streak became part of the neural plate. If this view were correct, which is accepted even by Rauber, the hypothesis I am attempting to establish would fall to the ground. I have, however, no doubt that these embryologists are mistaken. The very careful observations of Gasser show that the part of the primitive streak adjoining the embryo becomes converted into the tail-swelling, and that the posterior part is folded in on the ventral side of the embryo, and, losing its characteristic structure, forms part of the ventral wall of the body. On this point my own observations confirm those of Gasser. In the lizard the early appearance of the neurenteric canal at the front end of the primitive streak clearly shows that here also the primitive streak can take no share in forming the neural plate.

The above considerations appear to me sufficient to establish my hypothesis with reference to the nature of the primitive streak, which has the merit of explaining, not only the structural peculiarities of the primitive streak, but also the otherwise inexplicable position of the embryo of the amniotic vertebrates in the centre of the blastoderm.

On Certain Points *in the* Anatomy *of* Peripatus Capensis.

By F. M. Balfour, M.A., F.R.S.[1]

The discovery by Mr. Moseley[2] of a tracheal system in Peripatus must be reckoned as one of the most interesting results obtained by the naturalists of the "Challenger." The discovery clearly proves that the genus Peripatus, which is widely distributed over the globe, is the persisting remnant of what was probably a large group of forms, from which the present tracheate Arthropoda are descended.

The affinities of Peripatus render any further light on its anatomy a matter of some interest; and through the kindness of Mr. Moseley I have had an opportunity of making investigations on some well preserved examples of *Peripatus capensis*, a few of the results of which I propose to lay before the Society.

I shall confine my observations to three organs. (1) The segmental organs, (2) the nervous system, (3) the so-called fat bodies of Mr. Moseley.

In all the segments of the body, with the exception of the first two or three postoral ones, there are present glandular bodies, apparently equivalent to the segmental organs of Annelids.

These organs have not completely escaped the attention of previous observers. The anterior of them were noticed by Grube,[3] but their relations were not made out. By Saenger,[4] as I gather from Leuckart's 'Bericht' for the years 1868-9, these structures were also noticed, and they were interpreted as segmental organs. Their external openings were correctly identified. They are not mentioned by Moseley, and no notice of them is to be found in the text-books. The observations of Grube and Saenger seem, in fact, to have been completely forgotten.

The organs are placed at the bases of the feet in two lateral divisions of the body-cavity shut off from the main central median division of the body-cavity by longitudinal septa of transverse muscles.

Each fully developed organ consists of three parts:

(1) A dilated vesicle opening externally at the base of a foot.

(2) A coiled glandular tube connected with this and subdivided again into several minor divisions.

[1] From the 'Proceedings of the Cambridge Philosophical Society.'

[2] "On the Structure and Development of *Peripatus Capensis*," 'Phil. Trans.,' vol. clxiv, 1874.

[3] "Bau von *Perip. Edwardsii*," 'Archiv f. Anat. u. Phys.,' 1853.

[4] "Moskauer Naturforscher Sammlung," 'Abth. Zool.,' 1869.

(3) A short terminal portion opening at one extremity into the coiled tube (2) and at the other, as I believe, into the body-cavity. This section becomes very conspicuous in stained preparations by the intensity with which the nuclei of its walls absorb the colouring matter.

The segmental organs of Peripatus, though formed on a type of their own, more nearly resemble those of the Leech than of any other form with which I am acquainted. The annelidan affinities shown by their presence are of some interest. Around the segmental organs in the feet are peculiar cells richly supplied with tracheæ, which appear to me to be similar to the fat bodies in insects. There are two glandular bodies in the feet in addition to the segmental organs.

The more obvious features of the nervous system have been fully made out by previous observers, who have shown that it consists of large paired supraœsophageal ganglia connected with two widely separated ventral cords—stated by them not to be ganglionated. Grube describes the two cords as falling into one another behind the anus—a feature the presence of which is erroneously denied by Saenger. The lateral cords are united by numerous (5 or 6 for each segment) transverse cords.

The nervous system would appear at first sight to be very lowly organised, but the new points I believe myself to have made out, as well as certain previously known features in it, appear to me to show that this is not the case.

The following is a summary of the fresh points I have observed in the nervous system:

(1) Immediately underneath the œsophagus the œsophageal commissures dilate and form a pair of ganglia equivalent to the annelidan and arthropodan suboesophageal ganglia. These ganglia are closely approximated and united by 5 or 6 commissures. They give off large nerves to the oral papillæ.

(2) The ventral nerve cords are covered on their ventral side by a thick ganglionic layer,[1] and at each pair of feet they dilate into a small but distinct *ganglionic swelling*. From each ganglionic swelling are given off a pair of large nerves[2] to the feet; and the ganglionic swellings of the two cords are connected together by *a pair of commissures containing ganglion cells*.[3] The other commissures connecting the two cords together do not contain ganglion cells.

The chief feature in which Peripatus was supposed to differ

[1] This was known to Grube, loc. cit.

[2] These nerves were noticed by Milne Edwards, but Grube failed to observe that they were much larger than the nerves given off between the feet.

[3] These commissures were perhaps observed by Saenger (loc. it.).

from normal Arthropoda and Annelida, viz. the absence of ganglia on the ventral cords, does not really exist. In other particulars, as in the amount of nerve cells in the ventral cords and the completeness of the commissural connections between the two cords, &c., the organisation of the nervous system of Peripatus ranks distinctly high. The nervous system lies within the circular and longitudinal muscles, and is thus not in proximity with the skin. In this respect also Peripatus shows no signs of a primitive condition of the nervous system.

A median nerve is given off from the posterior border of the supracœsophageal ganglion to the œsophagus, which probably forms a rudimentary sympathetic system. I believe also that I have found traces of a paired sympathetic system.

The organ doubtfully spoken of by Mr. Moseley as a fat body, and by Grube as a lateral canal, is in reality a glandular tube, lined by beautiful columnar cells containing secretion globules, which opens by means of a non-glandular duct into the mouth. It lies close above the ventral nerve cords in a lateral compartment of the body-cavity, and extends backwards for a varying distance.

This organ may perhaps be best compared with the simple salivary gland of Julus. It is not to be confused with the slime glands of Mr. Moseley, which have their opening in the oral papillæ. If I am correct in regarding it as homologous with the salivary glands so widely distributed amongst the Tracheata, its presence indicates a hitherto unnoticed arthropodan affinity in Peripatus.

NOTES AND MEMORANDA.

Chlorophyll in Turbellarian Worms and other Animals.—Mr. Patrick Geddes has recently investigated the physiology and histology of the small green Planarian *Convoluta Schultzii*, and communicated his results in a highly suggestive paper to the Royal Society ('Proceedings,' No. 194). Mr. Geddes obtained these worms in large quantity at Roscoff, the zoological observatory of Prof. Lacaze Duthiers. He has succeeded in obtaining from a number of them, enclosed in an inverted glass vessel and exposed to sunlight, a quantity of gas which on analysis (by means of pyrogallic acid) proved to contain from 43 to 52 per cent. of pure oxygen. This is the first direct proof of the evolution of oxygen gas through the agency of the chlorophyll contained in the tissues of animals of so high an organisation as the Planarian worms; though it was from Euglena, an animal Flagellate that Priestley obtained oxygen gas, even before it was known to be given off by plants. The exact nature of the chlorophylloid substance has not been determined by Mr. Geddes. It has the general properties of the green colouring matter of vegetable tissues, but which of the constituents of that somewhat variable substance are present has not yet been determined. Leaving aside the unicellular organisms, we have at present knowledge of substances similar to leaf-green in the tissues of the Sponge Spongilla, of the Polyps Hydra, and *Anthea cereus*, of the Planarians *Vortex viridis* and *Convoluta Schultzii*, of the Gephyræan Bonellia, of the Chætopod Chætopterus and of the Crustacean Idotea. Of these cases only that of Spongilla and of Bonellia have been studied with special care as to their absorption spectra, and it is to Mr. Sorby's papers in vol. xv of this Journal that we must refer for a minute account of them. Mr. Sorby showed by spectroscopic evidence that the green matter of Spongilla contains the *same* constituents (though differing quantitatively) as do the leaves of green plants, namely, blue chlorophyll, yellow chlorophyll, orange xanthophyll, xanthophyll, yellow xanthophyll, and lichnoxanthine. In a later paper (this Journal, vol. xv, p. 166) he showed that the green colouring matter of Bonellia, though exceedingly close in spectrum and physical properties to the three species of chlorophyll distinguished by him

('Proc. Roy. Soc.,' vol xxv), viz. blue chlorophyll, yellow chlorophyll, and chlorofucine, is, nevertheless, distinct, and for it he proposed the name Bonelleine. The spectroscopy of the other cases of chlorophylloid substance in animals has not been worked out *in detail*, though I have shown that the absorption spectrum of the green colour of Hydra, of Chætopterus, and of Idotea, is similar in respect of its chief lines to that of the chlorophyll group.

Besides the facts as to (1) solubility; (2) fluorescence of the solution; (3) evanescence of the colour in sunlight; (4) position of the absorption bands; (5) optical and other properties of the products obtained by reagents, there are other highly-important classes of facts to be looked into in connection with the history of the chlorophylloid substances of animals. These are (6) the form and distribution of the green-coloured substance in the tissues of the animal possessing it; and (7) the evidences of its physiological activity (whether or not identical with that established for the chlorophyll of plants). Mr. Geddes showed, so far as this last point is concerned, that large quantities of oxygen were liberated by the green *Convoluta Schultzii*, and on the hypothesis that this was due to the breaking up of the CO_2 into O and CO under the influence of chlorophyll in sunlight, proceeded to search for evidence of the formation in the tissues of the Convoluta of starch or similar substances.

An analysis of the Convoluta *en masse* yielded evidence of the presence of ordinary vegetable starch in quantity. This, however, is not in itself a very striking fact. Sponges, devoid of chlorophyll, are known to contain in vacuoles of their constituent cells starch, so far as the blue reaction with iodine is evidence of the presence of that body,[1] whilst the glycogen reaction with iodine has been obtained from the tissues of a variety of animals (Tænia, Lamellibranchs, &c.). What one would like to be able to adduce as evidence of the physiological activity of the chlorophylloid substance of animals would be the appearance and disappearance of starch granules in close association with the green substance, and under such conditions as those established by Sachs in the case of the chlorophyll grains of higher plants. Unfortunately this is not possible in the case of Convoluta. Mr.

[1] See Keller, 'Zeitschr. wiss. Zool.', Bd. xxx, p. 574, 1878. He obtained, in a certain number of cells of various sponges, a blue coloration with iodine. The starch appeared to be in solution, and contained in large vacuoles occupied by the solvent. Keller found it in *Spongilla lacustris*, in *Reniera litoralis*, *Myxilla fasciculata*, *Geodia gigas*, *Tethya lyncurium*, *Suberites massa*, *Suberites flavus*. He failed, on searching, to find it in any Calcispongiæ, in Halisarca, and in Chondrosia.

Geddes gives important observations referable to our sixth category, from which it appears that the green substance of Convoluta does not exist in the form of grains, nor of fine granules, but "is diffused throughout the whole protoplasm" of certain cells, which lie *beneath the circular and longitudinal muscles*. Thus, the green substance of Convoluta differs most markedly from that of the allied *Vortex viridis*, in which it occurs in the form of *drops* in the cells; equally it differs from that of *Hydra viridis* and of Spongilla, which occurs in the form of grains embedded in the protoplasm of cells, the grains having the form of concavo-convex discs in Spongilla. In Bonellia, too, and Chætopterus the green substance is granular; in Idotea it is diffused. Nevertheless, Mr. Geddes obtained evidence of the formation of fine granules of starch in the green cells of Convoluta by the application of iodine to fresh-teased preparations of the worm's tissues. This we must regard as the most important part of the evidence which he is able to adduce in favour of the view that *Convoluta Schultzii* is actually nourished by the activity of its chlorophyll—that it, in fact, feeds on carbonic-acid as a green plant does.

It remains to be seen whether similar or even more conclusive evidence of this kind can be obtained from the examination of such chlorophyllaceous animals as Hydra and Spongilla.

Mr. Sorby, writing in 1875 in this Journal on Spongilla, said: "It would, I think, be well worthy of study to ascertain whether low animal forms which, like Spongilla, contain chlorophyll, have, when exposed to light, the power of decomposing carbonic acid, and supporting themselves, to some extent, as plants .... If so, they would be animals to some extent capable of plant-like growth, and would thus be the reverse of those plants which have lately attracted so much attention on account of their being able to partially support themselves by means of complex animal food, which they can digest and absorb like the most perfect classes of animals." Mr. Geddes's researches have established, in one case at least, what the mere fact of the presence of chlorophyll in animals had led naturalists to entertain as hypothesis. He remarks: "As the Drosera, Dionæa, &c., which have attracted so much attention of late years, have received the striking name of carnivorous plants, these Planarians may not unfairly be called vegetating animals, for the one is the precise reciprocal of the other. Not only does the Dionæa imitate the carnivorous animal, and the Convoluta the ordinary green plant, but each tends to lose its own normal

character. The tiny root of the Drosera and the half-blanched leaves of Pinguicula are paralleled by the absence of a distinct alimentary canal and the abstemious habits of the Planarian."

It is worth while pointing out that a considerable difficulty in relation to the view that the green specimens of *Hydra viridis* and *Spongilla fluviatilis* possess a vegetative nutrition, is presented by the fact that side by side with the green specimens occur very abundant *colourless* specimens, which appear to be equally robust and healthy. Do these colourless examples possess a colourless modification of chlorophyll which decomposes carbonic acid? or is the capricious distribution of the green substance analogous to the capricious distribution of Hæmoglobin, which is present, for instance, in the blood of Planorbis whilst absent from that of its associate Linnæus?

In connection with this subject it is important to notice that Metschnikoff has shown that in Rhabdocæl Planarians the individual cells of the enteric tract engulph food-particles, and thus reduce the digestive processes of these worms to the stage presented by colonies of amœboid organisms devoid of a true enteron, whilst Balfour has suggested that the nutrition of the sponges is effected by the cells of the ectoderm and by those of the endoderm; not, therefore, by aid of a digestive cavity. Mereschkowsky ('Ann. and Mag. of Nat. Hist.,' March, 1879) has adduced evidence in favour of a similar process, not only in Sponges but in Medusæ, the latter of which he has observed not unfrequently to be devoid of stomach and buccal aperture.—E. Ray Lankester.

A New Genus of Protista.—Prof. Sorokin, of Kasan, describes under the name *Gloidium quadrifidum* in Gegenbaur's 'Morph. Jahrb.,' Bd. iv, p. 399, a new naked protoplasmic organism devoid of nucleus, ·03 mm. in diameter, with vacuolated endosarc and hyaline periphery, which gives rise to lamellar pseudopodia, and possesses a pulsating vacuole. It was discovered in an aquarium containing Oscillariæ, Hormidia, &c. The specific name refers to its habit of multiplication by quadripartite division without encystation. Prof. Sorokin also observed the formation of a cyst around single individuals, which was not followed by division, but in many cases the organism escaped from the cyst by means of a small hole, which it appears to have the power of boring in the test with which it has previously covered itself.

PROCEEDINGS OF SOCIETIES.

Dublin Microscopical Club.

21*st November*, 1878.

Docidium hirsutum, Bailey, *occurring in Scotland, exhibited.*—Mr. Archer showed examples of *Docidium hirsutum*, Bailey, taken on the Deeside, in Scotland; it was very scanty indeed in the gathering, but Mr. Roy informed Mr. Archer that he had before encountered it. It seems to be scarcely happily named, as the roughnesses on the superficies partake, so to say, more of the character of elongate papillæ than of "hairs;" but Bailey speaks of it as "strongly hirsute," possibly in allusion to the coarseness of these "hairs"—a point perhaps rendering the identification of the form the more certain, but still his figure, in that case, shows the roughnesses as rather fine. It is not a very pretty form; the wall appears thick and somewhat opaque, and the green contents not of a lively tint. In these countries, at least, it must be surely a very rare species.

Section from an Enchondroma of Tibia, exhibited.—Mr. B. Wills Richardson exhibited two stained sections, one red, the other blue, taken with the freezing microtome, from an enchondroma that sprang from the head of the tibia of a young man. The tumour attained to a large size in a few months and amputation above the knee had to be performed. The case had a malignant history, death having occurred a year after the operation. The cells and their nuclei were large and there were one or two ossific centres in each section.

Exhibition of Octaviania asterosperma, Vitt.—Mr. Pim exhibited *Octaviania asterosperma*, Vitt. This, the first hypogæous fungus that Mr. Pim had met with, occurred in his garden at Monkstown, on a piece of old carpet that had been dug-in with manure. It appears to be but very sparingly distributed both in England and on the Continent, and is now, it is believed, recorded for the first time in Ireland.

Section of Dolerite, containing the new mineral Hullite, Hardman, *exhibited.*—Professor Hull, F.R.S., exhibited a thin section of the olivine dolerite of Carmoney Hill, near Belfast, containing the new mineral called "Hullite," by the discoverer, Mr. E. T. Hardman, who has given a description of it at the recent meeting of the British Association in Dublin (Section C). The mineral

occurs in grains filling cavities and small fissures in the rock. It is black, glossy, and has a conchoidal fracture, resembling pitchstone, but the chemical analysis shows it has no connection with this mineral, as it belongs to the ferrugino-chloritic group. With a 2-inch object glass it appears translucent, of a rich brownish yellow to bronze colour, sometimes traversed by dark prism-like bars. It is structureless or reticulated, filling cavities and the narrow fissures between the other minerals, which consist chiefly of unaltered olivine-plagioclase, a little augite, and a few grains of titano-ferrite. The mineral does not polarise, but with a higher power (1-inch objective) shows evidences of a reniform structure. The olivine in the rock is unusually fresh and polarises vividly.

Section of Spine of Salmacis rarissima, Agassiz.—Mr. Mackintosh exhibited a cross-section of *Salmacis rarissima*, Agassiz, one of the Acanthopneustes group, which though apparently monocycline in its mode of growth is not truly so, inasmuch as the solid wedges which make up the greater part of the spine exhibit a series of expansions at regular intervals indicating periods of growth.

Macro- and Microspores of Isoetes Morei, Moore, *exhibited*.—Dr. David Moore showed specimens of the macro- and microspores of his new species, *Isoetes Morei*, just described and figured in the 'Journal of Botany,' and contrasted the latter with those of the allied species *Isoetes setacea*, a native of the Mediterranean district.

December 19*th*, 1878.

Neomeris, undescribed species, shown.—Dr. E. Perceval Wright exhibited mounted specimens of a species of the genus Neomeris, collected in the Friendly Isles, by the late Professor Harvey. In the working collection of Dr. Harvey the species stood recorded under the manuscript name of *N. capitata*; from *N. dumetosa* of Lamarck it differed in very many respects, and from *N.* (*Decaisnella*) *nitida* of Harvey it differed, not only in being less calcareous, but in the beautiful regular hexagonal shape of the cells, and by the apparently one-celled stipes.

Section of Quartziferous Diorite of Quenast, shown.—Professor Hall, F.R.S., exhibited a section of quartziferous diorite of Quenast, kindly lent him by M. l'Abbé Reynard. In the crystalline grains of the silica were to be seen, by the aid of a high magnifying power (800 diameters), fluid cavities containing minute translucent cubes, inferred to be those of sodium chloride (or common salt), and about $\frac{1}{10000}$th of an inch in size. In one of the cells exhibited the vacuum bubble was observed close beside the crystal. The "diorite quartzifère" of Quenast is remarkable for containing these cubes, which have been also observed by Dr. Zirkel in the granite of Arran, in Scotland, and in other rocks.

New form of Cœlosphærium, inhabiting a flowering plant, shown.—Mr. Archer ex by Professor Alexander Dickson of the le plant, containing in the spaces examples of alga, morphologically, if the term be allo Nägeli's genus Cœlosphærium. It seeme ordinary pond species in the reddish-brown and in the elongate, not orbicular cells thes a proper cup-like, gelatinous support—the what like an acorn in its cup—this cup- appearing as if somewhat prolonged down pronounced a manner as may sometimes b form, met with in pools, *Gomphosphæria aponi* the form would appear to be heretofore unde unusual habitat may have something to say t similar allied forms occurring in the tissues are, however, now not rare. If one should form in a pond it would at once strike th Mr. Archer thought he might be justified in *Cœlosphærium Dicksoni*, after its discoverer.

Section of Spine of Phyllacanthus imperialis, intosh showed a cross-section of the spine *imperialis*, Lam., taken near the apex. It regularly stellate appearance, due to the proje of ridges on the surface, and had a very thick e

Crystals of Magnesian Phosphate from Urine, size, shown.—Dr. Tichborne showed crystals magnesian phosphate from urine, of remarkably the largest he had ever seen naturally deposited were 6 mm., and, being of a beautiful regularity, w suitable for polarisation.

16*th January*, 1879.

Section of Syenite, with imbedded slender prisms, disthene, shown.—Professor Hull, F.R.S., exhibited of a syenite (quartz, felspar, hornblende) from S containing long prisms of a greenish glistering mine to be disthene (kyanite), the analysis of which giv alumina 63·2 (Dana). This mineral was formerly Professor R. S. Scott, in Donegal. With a magnify about 225 diameters the grains of silica were see numerous fluid cells, together with long prisms abrupt Some of these prisms were also continued into the fel comparison to their diameters, were of great length a straight. Though generally colourless, they sometime shades of brown or umber. The mineral polarises vi supposed to be disthene. Olivine is also present.

Cutis vera from Heel, stripped of Epithelium, show Wills Richardson exhibited two blue-stained sections, ea

long, of the cutis vera (from the human heel), totally stripped of epithelium. The papillæ were thus perfectly exposed and in full relief. Sections of the heel were made with the freezing microtome last year, and he, being engaged with other matters, had to allow them to remain until recently, in glycerine and some Beale's carmine stain. To his surprise, when he examined them he found that the epidermis had separated from all the sections, possibly from the action of the ammonia of the stain, which was in excess. With some trouble he restained a few of them with anilin blue, two of which were those he exhibited. They were mounted in Farrant's solution, an excellent medium for anilin blue stainings, as he fancied it preserved the colour.

Pithophora Kewensis, transferred from Kew, and flourishing at Glasnevin, shown.—Dr. Moore showed a copious growth of *Pithophora Kewensis*, Wittr., in the normal healthy state, from a small supply sent from Kew in July, 1878, to Dr. E. P. Wright, and which Dr. Moore had placed in one of the tanks at Glasnevin, where it seemingly was inclined to flourish.

A probably new Cosmarium, shown.—Mr. Archer showed examples of what seemed to be either a new Cosmarium or a form of *Cosm. hexalobum*, Nordst., some from Scotland, prepared by Mr. Bisset; others from County Wicklow, obtained in Glencree. These specimens at least were absolutely identical, one and the same thing in the most minute detail, and Mr. Archer thought would really prove to be distinct from *Cosm. hexalobum*, besides being apparently decidedly smaller. It is, here, at any rate, a very rare form.

Eggs of Echinorhyncus, various stages, shown.—Dr. Macalister exhibited the eggs of *Echinorhyncus pinguis*, showing the early stages of the formation of the embryo of that species, the trilaminar egg-envelope, and the two kinds of blastomeres, into which the yelk segments. The formation of a central cavity was also visible in some of the more mature embryos.

Structure of the green normal leaves of Pinus monophylla.—Professor McNab exhibited transverse sections of the green normal leaves of *Pinus monophylla*. Usually in Pinus the normal leaves are reduced to thin scales in whose axils the short shoots with the needle leaves are developed. Frequently, however, in *P. monophylla*, these normal leaves, instead of being, as they sometimes are, mere scales, become large green flattened structures resembling the leaves of Abies. Such leaves, often with single needles or two needles in their axils, are frequent on young plants, on the newly formed shoots, both terminal and lateral. On transverse section these normal leaves are seen to be somewhat triangular, flattened above, but with a projecting midrib below. Both upper and under surfaces possess stomata. There are two resin canals in each leaf close to the epidermis of the under side, and about halfway between the rounded margin of the leaf and the projecting midrib. There is a single fibro-vascular bundle, surrounded by a distinctly marked sheath; the hypoderm is well-

developed. These normal leaves must not be confounded with the needle-leaves, which are produced in the axils of the larger or smaller normal leaves, either singly, in pairs, or in threes; in young plants either singly or in pairs, in old plants usually in threes. The single needles have a large central fibro-vascular bundle and well-marked sheath, surrounding a quantity of tissue belonging to the fibro-vascular mass. The stomata are placed in rows all round the cylindrical leaf. There are two resin-canals, and abundance of hypoderm is developed between the rows of stomata. The leaves in pairs are half-cylindrical, stomata on both surfaces, and with a small fibro-vascular bundle in a mass of tissue, surrounded by a circular sheath. The hypoderm is well developed, and there are two resin-canals in each needle. When in threes the needles are triangular, with a double fibro-vascular bundle and no resin-canals. The variation in the structure of the needles is remarkable, and the production of large green normal leaves seems to be a unique character, as yet quite overlooked by botanists.

20th February, 1879.

The stated meeting of the Club appointed for the above evening did not take place owing to the recent sudden and lamented death, on 3rd inst., of one of the members, John Barker, M.D., F.R.C.S.I.

20th March, 1879.

Fossil Calcareous Algæ and remarks thereon.—Dr. E. Perceval Wright exhibited specimens of *Cymopolia rosarium*, Lamr., and *Polytrypa elongata*, Defranc, side by side and called the attention of the Club to the very important memoir of M. Munier-Chalmas, "Sur les Algues calcaires appartenant au groupe des Dasycladées Harv. et confodues avec les Foraminifères," which was published in the 'Comptes rendus hebdomadaires of the French Academy of Science' for October 29th, 1877, and which opened up quite a new or almost a new field of research, which has been followed up by the same author in a note presented last month to the Geological Society of France, "On the genus Ovulites." Though regarded by some of the most eminent palæontologists as a monothalamic Foraminifer related to Lagena, the genus Ovulites is herein clearly demonstrated to be neither more nor less than an articulation of a siphonaceous alga having very close affinities to Penicillus.

Ovulites margaritula is described by Messrs. Parker and Jones "as a common Foraminifer of the 'Calcaire grossier.' Shaped like an egg, and when full grown, about the size of a mustard-seed, it is one of the most elegant of the fossil forms. The large terminal apertures, moreover, curiously impress upon the mind its resemblance to a 'blown' bird's-egg. [Written in

1860; nowadays birds' eggs are not thus blown.] It is the largest of the monothalamous Foraminifera. As a species it appears to have been short-lived. Fully developed in the deposits of Hauteville and Grignon it breaks in at once in the Eocene period. It lingers as an attenuated form in the Miocene beds of San Domingo. A recent Ovulite has not been met with. Scarcely another Foraminifer presents us with a similarly brief history—an undescribed form allied to Dactylopora affording almost the only parallel (namely, *Acicularia pavantina*, d'Arch.)."

In passing it may be noted that without doubt this last mentioned form is also only a portion of a calcareous alga.

The earlier memoir, of which the 'Comptes rendus' publishes only an extract, reminds us that it is not so very long ago (1842) since Prof. Decaisne demonstrated that a number of marine forms known as zoophytes, Corallina, Cymopolia, Neomeris, Penicillus, Udotea, Halimeda, &c., were in reality veritable algæ, but we may remark that Professor Schweigger, of Königsberg, had from actual observation of living specimens of several species of these calcareous algæ at Villefranche, come to the same conclusion in 1818 (Beobachtungen auf naturhistorichen Reisen. Anat.-phys. Untersuchungen über Corallen,' Berlin, 1818), and if one were to go back to the pre-Linnean times Ray (1690) described Corallina as "plantæ genus in aquis nascens," and Spallanzani, Carolini, and Olivi, even maintained the same against the peculiar reasonings of Ellis, the authority of Linneus, and despite the conversion of Pallas; but so influenced by authority were, apparently, most botanists down to 1842, that a Professor of Botany in the Edinburgh University (Graham) politely requested, it is said, the zoologists to keep *their* Cryptogamia to themselves, and a Professor of Botany in the Dublin University (Harvey), in the first edition of his 'Manual of British Algæ' (1841), did not include any of the Corallines. Since the memoirs of Decaisne and Chauvin, all this has changed, and we imagine that there is now no difference of opinion existing among botanists as to the general affinities of the living forms of calcareous algæ.

M. Munier-Chalmas in his memoir demonstrates that there must be also added to this group a numerous series of fossil forms which the old authors placed among the polyps, and which most of the modern writers on the subject have ranked among the Foraminifera. Bosc, in 1806, described and figured ('Journal de Physique,' Juin, 1806) some fossil organised bodies under the name of *Rétéporites ovoides*, for which bodies Lamarck, in 1816, established the genus Dactylopora. "The most singular varieties of opinion have existed," writes Dr. Carpenter in his well-known 'Introduction to the Study of the Foraminifera,' as to the true character of these fossil organisms. In separating them generically from Retepora Lamarck still associated them in the same group of supposed zoophytes; this position was also

accepted for the genus by De Blainville and Defranc." [It is but justice to De Blainville to point out that he quotes without disapproval the statement of Schweigger, "que les dactylopores et les ovulites ne sont rien autre chose que des articulations d'une grande espèce de cellaire, analogue à la cellaire salicorne"]. "In 1852 Dactylopora was included among the Foraminifera by d'Orbigny, who showed, notwithstanding, by the place he assigned to it, a misapprehension of the real nature scarcely less complete than that under which his predecessers had lain; for he ranks it in his order Monostègues, next to the unilocular Ovulites, and says of it: 'c'est une Ovulite également percée des deux bouts, pourvue des larges pores placées par lignes transverses.' How utterly erroneous is this description will appear from the details to be presently given, yet d'Orbigny's authority has given it currency enough to cause it to be accepted by such intelligent palæontologists as Pictet and Bronn, who in the latest editions of their respective treatises have transferred Dactylopora to the place indicated by him, not, however, without the expression of a doubt on the part of Bronn as to whether the true place of the genus is not among the Fistulidæ in alliance with Synapta and Holothuria—a suggestion that indicates a perversion of ideas on the subject for which it is not easy to account. The complex structure of the organism in question was first described and the interpretation of that structure on the basis of an extended comparison with simpler forms was first given by Messrs. Parker and Jones in so unobtrusive a manner as scarcely to challenge the attention which their investigations deserve, and I gladly avail myself of the opportunity which the present publication affords to give a fuller account, with the requisite illustrations of this remarkable type, the elucidation of which seems to me not unlikely to lead to a reconsideration of the place assigned to many other organisms at present ranked amongst Zoophytes or Polyzoa;" and then follow nine pages of a most elaborate description of every ridge and furrow, of every elevation and depression to be met with in any of the so-called species, so that probably no single vegetable cell was ever before so minutely described.

The genus is placed the eleventh in order of the family Miliolida, a family which contains some of the most typical of Foraminifers. "It may be conjectured without much improbability," writes Dr. Carpenter, "that Dactylopora is only the single representative of a group whose various forms filled up the hiatus which at present intervenes between itself and its nearest allies among the ordinary Foraminifera." But, writes M. Munier-Chalmas, "the study and comparison of species of Dasycladus, Cymopolia, Acetabularia, Neomeris, &c., in the herbarium of the museum, and in that of M. Ed. Bornet, who placed without reserve at my disposal his library and collections of these plants, proved to me that the species of Dactylopora, Acicularia, Polytrypa, &c., are decidedly algæ, very nearly allied to species of

the recent genera just quoted, if not identical therewith." The accompanying figures of specimens exhibited show plainly, for example, that the genera Cymopolia and Polytrypa may be

CYMOPOLIA AND POLYTRYPA.

FIG. 1.—Transverse section of a morsel of the calcareous tube of *Cymopolia rosarium*, Lamr., showing the canals which receive the whorl of cellules and the central sporangial cavity.

FIG. 2.—Transverse section of *Polytrypa elongata*, Defrance, showing the same portions.

FIG. 3.—Part of a whorl of cellules of *Cymopolia rosarium*, separated from the calcareous tube by acid. A, Wall or central cellule; B, first row of cellules; C, terminal whorl of cellules, in the centre of which is D, the axillary sporangium.

FIG. 4.—Exactly the same parts in *Polytrypa elongata*, obtained from a mould.

united; for the typical species thereof offer in every respect the same generic characters, and there is even a difficulty to find for them sufficiently distinct specific characters. Under the denomination of "*Siphoneæ verticillatæ*," M. Munier-Chalmas unites (1) "Those green-spore bearing algæ arranged by Harvey in the family of the Dasycladeæ; (2) All those fossil genera related to Larvaria, Clypeina, Polytrypa, Acicularia, Dactylopora, and Uteria. This group at present contains over fifty genera, which are for the most part to be met with in the triassic, jurassic, cretaceous, and tertiary strata. In the number of those actually living there is a notable falling off, there being not more than the seven following genera:—Dasycladus, Halicoryne, Cymopolia (with two sub-genera, Polytrypa and Decaisnella,[1] g.n.), Polyphysa, Acetabularia, Neomeris, and Bornetella,[2] g.n." [Doubtless a few more genera of recent forms yet remain to be de-

[1] Type, *Dactylopora eruca*, Parker.
[2] Type, *Neomeris nitida*, Harv. MS.

scribed. Thus Chloroclados, of Sonder, appears to be a good and distinct genus allied to Dasycladus.]

"The frond in the *Siphoneæ verticillatæ* is simple or dichotomous; it consists of a central tubula unicellular axis, around which are arranged the radiary and verticellate ramuli, the exact arrangement of which varies according to the genera and to the species. In most of the species carbonate of lime is found deposited in abundance in the outer walls of the main axis and its ramuli, and this forms around the plant a calcareous envelope, in which is reproduced all the details of its organisation. This mineral coating may consist of one or of two calcareous cylinders. The inner cylinder will be formed by the central axis and the first row of cells which arise therefrom. The outer cylinder is laid down by the most external of the verticels of cells; these terminate by a splayed-out enlargement, the lateral edges of which become more or less consolidated with the similar enlargements of neighbouring cells, and by thus causing a reciprocal pressure very regular hexagonal surface markings are produced. The organs of fructification are themselves surrounded by calcareous material, and assist in the formation of the outer cylinder, a fact easily seen in any section of Cymopolia.

"The result of such an organisation is that when the organic vegetable matter becomes destroyed there still remains in those fossil species, which laid down a great deal of calcareous material, as well as in those living species, which lay down more or less of it, a skeleton permeated by canals (rays of the ramuli) and chambers (fructification). This arrangement, which permits of an exact classification of the fossil species being wrongly interpreted, led even some most distinguished authors to see in these morsels of plants the full organisation of a Foraminifer."

Here it seems desirable to add that the conclusions of the author on this subject are in every particular acquiesced in by one in every way thoroughly able to judge of the facts, Dr. Ed. Bornet, and on a careful study of the specimens shown, which were prepared by Dr. Bornet, and for which Dr. Wright took this opportunity of thanking him, it was scarcely possible to conceive the demonstration as admitting of a doubt.

Mounted specimens of nearly all the recent species were also exhibited.

Coloured Drawings by the late Mr. Stewart, of Edinburgh, of some Rupicolous Algæ, exhibited.—Professor McNab showed some beautifully executed coloured drawings by the late Mr. Stewart, of Edinburgh, for Mr. Jenner, of that city, of certain rupicolous algæ—*Glœocapsa sanguinea* and others. Amongst these was one of a filamentous form, evidently, on the one hand, related to Scytonema, and on the other, by reason of its tapering filaments, related to Rivularia. A speciality seemed to be that groups of filaments occurred spirally curved and intertwined, giving the aspect of, as it were, a great cable, the scale upon which the drawing was made being large, probably 600 diameters.

The cells seemed to form a single file, mode of branching not evident. The probably inner and older portions of the mass appeared colourless, whilst the seemingly more vigorous portions showed a brown colour; the sheath very thick. This curious form (with the rest) was found on rocks in Arran.

Cosmarium acanthophorum, Nordstedt, *exhibited.*—Mr. Archer showed an example from Professor Nordstedt's hands of his so-called *Cosmarium acanthophorum*. Why he refers this form to Cosmarium at all, and not to Xanthidium, Mr. Archer could not see, as it seemed undoubtedly to come under the latter genus, just as decidedly as do *Xanthidium aculeatum*, *X. Nordstedtii*, or the common *X. antilopæum*. Mr. Archer showed in illustration *Xanthidium aculeatum* side by side.

Exhibition of Helminthosporium echinulatum, Berk.—Mr. Greenwood Pim showed *Helminthosporium echinulatum*, Berk., which occurred in considerable abundance on the frost-killed, though not fallen, leaves of *Eucalyptus globulus* in his garden at Monkstown. It is a very distinct form, being the only one of the genus in which echinulate spores are found. It seems to be rare, as Cooke quotes but one authority, viz. Rev. M. J. Berkeley, in 'Gardeners' Chronicle,' 1870, who found it on carnation-leaves—a locus for numerous microscopic fungi. The plant shown accorded exactly with Berkeley's figure.

Exhibition of Section of Testicle—Mr. B. Wills Richardson exhibited two complete sections of the testicle, with portion of the epididymis of a boy nine years of age. They were made with the freezing microtome and were cut from before backwards parallel to the side of the organ, were unbroken and exceedingly thin. One was an anilin blue staining, the other a picro-scarlet made with picric acid and a scarlet obtained from Messrs. Brooke, Simpson, and Spiller, of London. This section was first stained with an alcoholic solution of the picric acid, then washed in rectified spirit and subsequently coloured with an alcoholic solution of the scarlet. Half an hour or so sufficed for the process. When sufficiently stained with the scarlet, the section was again washed in alcohol and finally mounted in dammar solution.

Section of Quartzite from Nephin.—Professor Hull, F.R.S., exhibited a thin section of the micaceous quartzite of Nephin. It is of a light grey colour, exhibiting slight traces of foliation, and containing numerous minute flakes of mica. The plane of the section is at an angle of about 25° to that of foliation. With 2-inch objective the mass appears to consist of colourless, translucent quartz, with numerous elongated crystals of mica, lying in nearly parallel directions. With the polariscope the silica resolves itself into distinct granules, irregular in form and polarising vividly, particularly with crossed Nicols, when it shows a variegated field of purple, blue, yellow, pink, light yellow, light blue colours. The mica also polarises and shows the usual deep scars of the planes of cleavage. With $\frac{1}{5}$ objective minute cells

are seen in the silica. It is clear that the original grains of sand of which the rock was formed before metamorphism still retain their individuality.

At the close of the meeting the following Resolution was passed:—*Resolved* that "the Club desire to place on record their sense of the great loss which they have sustained by the sudden death of their ordinary member, Dr. John Barker. He was a long esteemed and much valued colleague, always ready for any act of friendly kindness, genial and warm-hearted, faithful and true. By those of the Club who knew him long and intimately, as well by the pond-side as by the fire-side, he will be equally missed and regretted, nor can his place among us be ever filled by one more sincere to his friends or to everything he thought honest and upright."

MEMOIRS.

On some Points *in the* Early Development *of the* Common Newt. By W. B. Scott, B.A., Fellow of the College of New Jersey, Princeton, and Henry F. Osborn, B.A., Princeton. (With Plates XX and XXI.)

The present paper records a series of observations on the development of *Triton tæniatus* (and partially also *T. cristatus*), made by the writers in the Morphological Laboratory of the University of Cambridge.

It deals chiefly: (1) with the formation and character of the germinal layers; (2) the development of the notochord; (3) the extension of the body cavity into the head, and the formation of mesoblastic somites in that region; (4) the development of the thyroid body.

With a view of making the following account as clear as possible, we have chosen a series of embryos showing the most important steps in development, and have designated the stages which they represent by letters in imitation of the plan adopted by Mr. Balfour in his 'Monograph on the Development of the Elasmobranch Fishes.' And we have further endeavoured to make these stages correspond to those of *Bombinator igneus*, as figured by Dr. Götte[1] in his great work. As might be expected, Triton in many ways shows a close resemblance to the Batrachian,[2] and yet at the same time it presents a number of curious and striking differences from that type. In order to elucidate these we have followed Dr. Götte's arrangement as far as practicable.

The preparation of the Triton embryos was attended with considerable difficulty. It was found in all cases advisable to remove the albumen from the ovum before hardening. The vitellus is quite liquid, and the vitelline membrane is so excessively delicate that this operation must be conducted

[1] A. Götte, 'Entwickelungsgeschicte der Unke.'

[2] The term "Batrachia," is used in this paper in the restricted sense as equivalent to the *Anurous Amphibia*.

with the greatest care; and as the albumen is permeated by several membranes, it was found necessary to cut these with fine scissors before the embryo could be with safety extracted. Many hardening reagents were experimented with—osmic acid, bichromate of potash, Müller's fluid, &c., but the most satisfactory one proved to be Kleinenberg's picric acid, with which nearly all the embryos described in the following pages were prepared. In those cases where the entire egg was hardened without previously removing the albumen, the results were most unsatisfactory. Kleinenberg's hæmatoxylin was the staining fluid employed for the sections.

A.

This includes embryos intermediate in age between Götte's figs. 39 and 40, taf. iii. The blastospore is quite small, a narrow groove, the "Rückenrinne," running forward some distance from its anterior edge. The medullary folds do not as yet appear in surface views. The ovum is still almost perfectly spherical in shape.

B (Unke, Taf. iii, figs. 40 and 41).

At this stage the medullary folds become well developed and very plainly marked. As yet they are widely separated. The medullary plate is formed, but the groove which divides it into two parts does not reach far forwards of the middle; or, any rate, if present anteriorly, is extremely faint. The ovum has elongated very slightly, but still appreciably.

C (Taf. iii, fig. 42).

The medullary folds now become still more pronounced, and begin to approach each other. The point of closest approximation is in the region which will eventually become the neck, and here is the first point of contact, just as it is in the Batrachia. The medullary plate is plainly divided throughout. The elongation of the embryo is not much more marked than it was in the previous stage.

D (see Pl. XXI, fig. 16).

Up to this stage no important external differences between Triton and Bombinator are apparent, but now a number of points of divergence begin to be noticeable. The medullary folds have closed throughout the region of the trunk, but still remain open in the head. Posteriorly they separate to form a *sinus rhomboidalis;* this does not seem to be merely a part of the canal which has not yet closed, but a genuine

dilatation. It is either absent or very transitory in Bombinator. As the folds enclose the blastopore, which remains open till a much later period, the sinus gives a communication from the exterior to the alimentary canal. When the sinus closes there is still the communication between the neural and alimentary canals, which has now been observed in so many types (Amphioxus, Accipenser, Elasmobranchii, Bombinator, &c.). The elongation of the embryo becomes very decided, and one surface of it becomes nearly flat; in Bombinator this is the dorsal surface; in the Newt it is the ventral, so that the latter is curved over the yolk. This difference is due merely to the larger amount of food-yolk in the egg of the Urodele, and cannot be considered of any great morphological significance. The bearings of the increased quantity of food-yolk will be discussed further on.

E.

This stage includes embryos, perhaps not quite so far advanced as the one figured in Götte's Taf. iii, fig. 50. The closure of the medullary folds is now complete throughout, and the vesicles of the brain are obscurely marked. The cranial flexure is already decided, and the whole embryo is somewhat curved upon itself, causing the ventral surface to assume a concave outline (except posteriorly, where the large mass of yolk produces a bulge). A trace of the opening of the sinus is still apparent.

F (Taf. iii, fig. 52).

The ventral curvature now becomes stronger, as does also the cranial flexure. The curvature is in an opposite direction to that taken by Bombinator. The vesicles of the brain are very distinct, and the optic vesicles which commenced in the last stage are now remarkably large, much more conspicuous than in the Bombinator of corresponding age. Another difference presents itself in the fact that in the latter the optic vesicle is an elongated oval, while in the former it is hemispherical. The rudiments of the fifth and seventh pairs of cranial nerves appear as buds from near the dorsal part of the hind brain, higher up than in Bombinator. A few protovertebræ have been formed. Up to this time there has been little or no increase in absolute size, the changes in form being produced by the elongation and narrowing of the embryo.

G.

In this stage the cranial flexure is carried further, and the head, as a whole, has taken a spherical shape, very differen

from the shape assumed by the Batrachian head. The rudiments of the visceral arches appear, and the tail begins to bud out from the yolk sac as an unsegmented mass of mesoblast. The number of somites has increased.

H (Taf. iii, fig. 53).

The elongation of the embryo has now progressed to a very considerable extent. The cerebral hemispheres bud out as an unpaired rudiment from the forebrain. Four visceral arches and three clefts have been formed. The tail has elongated somewhat, and is still unsegmented. We have been unable to discover anything of the suckers or horny teeth found in the Batrachian larvæ.

I (Taf. iii, fig. 54). (See also Pl. XXI, fig. 17).

This stage exhibits a general advance in development, but the only new feature is the appearance of the involution for the mouth. This is transversely elongated, differing from the mouth involution of Bombinator. The head shows swellings, which correspond in position to those which Götte has named, respectively, kidney swelling, lateral nerve, seventh and fifth nerves, auditory vesicle, and Gasserian ganglion; but, owing to the fact that the curvature is in the opposite direction, these organs are separated by wider intervals than in Bombinator.

We shall have occasion to refer to one or two later stages (K and L), which are marked by general increase in size, the formation of the lens, and the appearance of the external gills.

Segmentation and Formation of the Layers.

We have not succeeded in securing a complete series of specimens showing all the stages of segmentation, but from those which we have observed there can be little doubt that it proceeds very much in the same manner as in the Frog. Segmentation is asymmetrical, and this characteristic begins to appear at a very early period. The earliest stage we have seen shows two longitudinal furrows, which cut each other at right angles at the upper part of the egg, and passing down the sides, gradually fade and disappear before reaching the lower pole. The food-yolk even at this period preponderates in the lower part of the egg, and thus prevents the yolk-division taking place so rapidly as it does above. These furrows may be compared to two meridians on a globe; the next one (judging from the analogy of the Frog) represents the equatorial furrow in Amphioxus, but, for the reason above

stated, it is much nearer to the upper pole than to the lower, and this gives at once the distinction of larger and smaller blastomeres. The smaller blastomeres grow round the ovum over the larger, and bear the same relation to them as they do in the Frog. The segmentation cavity appears early, and from the very first its roof is only one cell thick, just as in the case of the Lamprey. As we shall see later the epiblast is at first composed of one layer, and hence the roof of the cavity is covered by epiblast only. In the Elasmobranch Fishes the roof of the cavity is formed by lower layer cells also, and this Mr. Balfour explains by the increase in the quantity of food-yolk in the cells, compelling them to creep up the sides of the cavity. Although there is proportionately more food material in the Newt's egg than in that of the Frog the increase is relatively small and does not affect the position of the cells. The only difference between the two at this stage consists in the fact that the roof of the cavity in the Frog is two or more cells thick, and in the Newt only one. In short, the ovum of the latter resembles the morula of Amphioxus with a large amount of food material stored away in its lower part. Judging from the descriptions of Calberla, it is in no way different from the ovum of Petromyzon of corresponding age. The floor of the segmentation cavity, as in all ova which contain food-yolk, is formed by the upper layer of yolk-cells from which, eventually, the ventral epithelium of the alimentary canal is in part derived.

The next step in development is, as in the Batrachians, a process of invagination, and, as in them, it is an unsymmetrical invagination. The disturbing cause is in both cases the presence of the food-yolk below. Owing to the fact that the food to be made available must be placed upon the ventral side of the body, the invagination must in this region take place very slowly or not at all. By this simple consideration Mr. Balfour explains the unsymmetrical gastrula of the higher Vertebrates.

At the period when our study of the two lower layers proper begins, segmentation is complete; the lips of the blastopore are rapidly nearing each other; the epiblast consists of a single layer of partly columnar, partly wedge-shaped, cells, and has already in great measure attained those characters which persist throughout several of the following stages.

At the lip of the invagination (see Plate XX, fig. 2) there is a decided swelling produced, in part by a lengthening, in part by a reduplication of the cells, a histological change

analogous to that which has been pointed out in the so-called embryonic rim in the Elasmobranchs.[1] The cells have a radiated arrangement, losing as they are reflected inwards their columnar character and becoming more spindle-shaped. As they approach the inner side of the lip they are quadrate, then oblong, then columnar, their outer ends abutting against the inner ends of the long epiblast cells. As the sections pass into the lateral region of the embryo, this relation is lost, and confluent with the forming hypoblast cells are the parent mesoblast cells. The latter may fairly be considered to arise actually from the point of invagination and not as a secondary splitting off from the hypoblast on either side.

Two longitudinal sections of an embryo at this period have been figured in Plate XX, figs. 2 and 3. Fig. 2 represents a section passing through the median line, and those changes in the epiblast at the lip of the blastopore which have been just referred to, may be followed. The alimentary canal has not proceeded far forwards, but the cells of the upper yolk are plainly forming the future hypoblast cells. The segmentation cavity is being pressed downwards; the section is in the median line behind and out of the median line in front. The reverse is true of the succeeding section (fig. 3), which represents the growth of the mesoblast at the sides of the invagination and the actual forward progress of the alimentary canal in the middle line. It illustrates the position and advancing obliteration of the segmentation cavity. Comparing the two sections, a very fair idea can be formed of the advance of the embryo in the early part of the stage (A).

The process at the *sides* of the median line in Triton is then homologous to that which Götte[2] represents as occurring in the median line in Bombinator, a construction which aids him in carrying out his peculiar views of the development of the notochord from the mesoblast.

Calberla,[3] on the contrary, describes as the immediate result of invagination, in *Rana temporaria*, the primary entoderm. This does not split in the median line, while at the sides it splits soon after formation, to give rise to the lateral plates of mesoderm. A fuller notice of his views will be given later.

[1] *Vide* Balfour, 'Elasmobranch Fishes,' chap. ii, p. 43.

[2] *Vide* Alexander Goette, "Entwickelungsgeschichte der Unke," 'Atlas,' Tafel. ii.

[3] E. Calberla, "Zur Entwickelung des Medullarrohres und der Chorda-dorsalis der Teliostier und Petromyzonteu," p. 261, 'Morphologischen Jahrbuch,' 3, 1877.

Our sections do not wholly accord with the observations of either of the above, for if it is clear that the invagination gives rise in the median line to a single layer of cells, it is equally clear that at the sides it gives rise to a double layer, namely, of mesoblast as well as hypoblast.

The process in Triton agrees then more closely with that occurring in the Elasmobranch Fishes,[1] where the lower layer cells, confluent with the reflected epiblast on either side of the axial line, form a layer of spherical cells above and columnar cells below, and the former is ultimately separated off as the mesoblast proper, while in the axial line the lower layer cells give rise simply to a columnar layer.

Now, turning to the transverse section of a Triton embryo Stage A (see Plate XX, fig. 4) we find that it adds still further probability to this view, for the relations of the layers fully accord with the above interpretation of the invagination.

Now, as concerns the further growth of the mesoblast, it results from the foregoing conclusions concerning the hypoblast that the mesoblast is never present across the axial line in the early stages. In transverse sections of Stage A it appears as two lateral plates extending on either side to a point just above the side limits of the alimentary canal. The layer where it is nearest the alimentary canal consists of small round cells, one or two deep, which can be readily distinguished from the adjacent hypoblast. These are the cells which we have just referred to as having resulted from invagination, and we shall speak of them hereafter as the primary mesoblast cells.

In conclusion, all the observations we have made favour the above interpretation, while none in any way disprove it.

Thus, at once three important distinctions are established between the development of the layers at the point of invagination in Triton and Bombinator, if we accept in full Dr. Götte's investigations of the latter. First: in Triton there is a decided thickening of the single layered epiblast as it approaches the point of invagination. In Bombinator there is none. Second: the resulting hypoblast in the axial line is in direct contact with the epiblast. There is no intervening mesoblast as in Bombinator. Third: the mesoblast is found in Triton as two lateral plates, and is not continuous across the middle.

These observations, coupled with those of Calberla, we think leave little doubt that Götte has mistaken the upper hypoblast cells for mesoblast, and thus at the start fallen into an

[1] *Vide* F. M. Balfour, 'Elasmobranch Fishes,' p. 49.

error which involves some of his subsequent conclusions in doubt.

Having thus briefly considered the origin of the two inner layers, as related to the phenomena of invagination, we shall return to the history of the epiblast from the beginning, and resume our discussion of the mesoblast and hypoblast in the subsequent pages.

General Features of the Epiblast.

When the epiblast can first properly be said to be formed, it consists of a single layer of very large quadrate cells, with large clear nuclei. In the next stage, when the invagination first commences, the cells have somewhat lengthened out, but are still very broad (Plate XX, fig. 1). When the invagination has progressed considerably, and the segmentation cavity has been much narrowed, we find that the cells have assumed the condition which they retain for some time after this. They are long, narrow, and columnar; most of them can be traced through the layer from one surface to the other without any change of size, although here and there several may be seen which have a wedge-shape, and alternate arrangement with their neighbours. The nuclei, however, are arranged in two rows, like those of the Elasmobranch epiblast. In general appearance, up to this time, the epiblast is more like that of Petromyzon than of any embryo which we have seen,[1] but the arrangement of the cells is somewhat more regular. For a short time, indeed, the appearance of the two is almost identical, but in the Newt the cells speedily become narrower, and more columnar in character, and the nuclei assume the alternate arrangement which is only faintly indicated in the Lamprey. During Stage A, when the medullary groove has begun to make its appearance, the middle line of the dorsal epiblast, exhibits a decided thinning to form the groove (Plate XX, fig. 4). But this grove is not at this period, nor do we find it afterwards, nearly so deep or so wide as it is in the Elasmobranchs.[2]

The next change of importance takes place during Stage B (Plate XX, fig. 5), when the medullary folds are well formed. These folds are caused by the multiplication of cells of the epiblast, which here becomes much thickened. Although the folds are several cells thick they show no indication of being separated into different layers. With the excep-

[1] See a paper by Calberla, 'Morph. Jahrbuch,' 1877, 3, taf. xii, fig. 7.
[2] Balfour, loc. cit., plate iv, fig. 8 a.

tion of the medullary plate the remainder of the epiblast shows no especial change from the condition seen in the preceding stage. In the medullary plate, on each side of the middle line, is a low rounded ridge (Plate XX, fig. 5), which is formed by the increase in length of the epiblast cells, and perhaps partly also by the wedging in of the mesoblast along these two lines.

The condition of the spinal cord at this period recalls the the condition of the same organ in the Batrachia of this age. For in the latter the nervous and epidermic layers fuse together into one indiscriminate mass, and do not separate again till much later. This separation takes place for the first time in Triton, not far from the age in which it reappears in the Batrachia. During Stage c sudden and rapid changes make their appearance. The medullary folds are now very prominent, and are composed of numerous elongated spindle- and wedge-shaped cells, while in many places the medullary plate shows a commencement of the same process (Plate XX, fig. 6). But as yet in neither of these regions are any distinct layers to be seen. The lateral epiblast is just beginning to separate into two layers ; the process commences immediately outside of the medullary folds, and spreads down the sides of the embryo, until it has been completed all around (fig. 6). Plate XXI, fig. 9, shows a drawing on a larger scale of the point where such changes are going on most actively. Even with the aid of this we have not thoroughly satisfied ourselves as to the exact manner in which these changes are accomplished. Three suppositions may be made with regard to it—(1) that the upper layer splits off from the lower by a process of cell division ; (2) that the wedge-shaped cells draw in their edges, and lying in alternate arrangement come to make two rows, one above the other ; (3) that both of these have their share in the process. On the whole we rather incline to the latter opinion. In favour of the alternate decrement of length is the fact that for some time preceding the separation the nuclei of the cells are arranged in two alternate rows, very much as in the Elasmobranchs, while such an appearance as shown at the point *a*, fig. 9, looks as if it could only be cell division.

Turning to Stage D (Plate XX, fig. 7), we find that in the trunk region the medullary canal is completely closed, and the division of the epiblast carried entirely around the embryo, giving us two well-marked layers. These are composed of quadrate, somewhat flattened cells, of nearly equal size in both layers. The cells composing the spinal cord

are numerous, elongated, wedge- or spindle-shaped; but even yet there is no indication of distinct layers.

As in the Bird, the Mammal, and the Elasmobranch Fish, the epithelium lining the spinal canal does not become differentiated till a considerably later period.

As a whole the spinal cord is now a hollow cylinder with very thick walls and a very small lumen. It presents a transversely oval section, and is somewhat indented on its lower surface by the pressure arising from the notochord. The epiblast has met and coalesced along the middle line above the canal, though a slight groove still shows the line of union.

From this time forward the outer layer of the general epiblast becomes flatter and flatter, while the inner layer grows more columnar. But in those parts of the skin which cover the brain both layers are composed of very much flattened cells (Pl. XXI, fig. 13). The inner or mucous layer, when once formed, is the active layer, and from it alone such structures as the lens of the eye are derived.

The primitive condition of the epiblast in Triton is an extremely interesting one, presenting in a somewhat unexpected manner great differences from that of the Frog. As is well known, in the latter animal the epiblast is double-layered from an extremely early period, the roof of the segmentation cavity being formed by two layers of cells, and by the time of invagination there is an outer stratum of a single row of flattened cells and an inner stratum of several rows of rounded cells, the epidermic and nervous layers of Stricker. "Both strata have a share in forming the general epiblast, and though eventually they partially fuse together, there can be little doubt that the horny layer of the adult epiblast, when such can be distinguished, is derived from the epidermic layer of the embryo, and the mucous layer of the epiblast from the embryonic nervous layer. Both layers of the epiblast assist in the formation of the cerebro-spinal nervous system, and they also at first fuse together, though the epidermic layer probably separates itself again as the central epithelium of the spinal canal." (Balfour, loc. cit., p. 99.)

All this is very different from what we see in Triton. At first the epiblast is of one layer, and so remains for a considerable time; the mucous layer, when formed, consists of a single stratum of more or less columnar cells, and the epithelium of the spinal cord appears for the first time at a much later period. In short, the condition of the epiblast, except in the last respect, is more like that of *Petromyzon* than that

of the *Batrachia*. It is, as might be expected, intermediate between the two types in many ways. In the Lamprey the division into two layers does not occur until a comparatively late period, some time after the larva has been hatched, while in the Newt it occurs as early as Stage c. In the Frog it is found from the first. Another respect in which the Newt is intermediate is the histological character of the layers. The Elasmobranch Fishes in this respect present an intermediate condition between the Lamprey and the Newt. In them also the epiblast is primarily single; the first change consists in the part which will give rise to the central nervous system, becoming several cells thick, but presenting no distinction into two layers. Eventually, later than in the Newt, earlier than in the Lamprey, the epiblast divides into mucous and epidermic layers. Both layers seem to enter into the formation of the organs of sense, while in the Amphibians the sense organs are formed exclusively, or almost so from the mucous layer, and in the Lamprey they are derived from the epiblast before its division into the layers.

These facts put us in a somewhat favorable position for the solution of the question as to whether the single- or double-layered epiblast is the primitive condition. We are decidedly of the opinion that the conclusion drawn by Mr. Balfour on p. 100 of his book on the Elasmobranchs is the correct one, viz. that the single-layered epiblast is the more primitive condition. He was not aware at that time of the difference existing between the Frog and the Newt in this regard, and so attributed the double layer to the Amphibians generally. But, as we have seen, it is confined to the Batrachians, a much more restricted group, and is, perhaps, also found in Osseous Fishes. Besides these it is found in no other groups of the animal kingdom, and, as Mr. Balfour points out, it is more probable that a particular feature of development should be thrown back to an earlier period than for the distinction between the two layers to be absolutely lost, and then to reappear at a later stage. This *à priori* consideration receives a great deal of support from the facts of the development of the Newt. By its aid we are enabled to arrange a series of steps of advancing differentiation of the epiblast from Amphioxus through the Marsipobranchs, the Elasmobranchs, and the Newt, to the Batrachians.

The steps of this progression have been already stated, but it may be well to summarise them. (1.) Amphioxus has an epiblast consisting at first of short columnar cells in a single row. These afterwards begin to flatten out, and in the adult are very much flattened, *but never constitute more than a*

single row. The medullary plate is the only epiblastic development which consists of more than one row of cells. This fact alone is of considerable weight in the question we are considering; and it should be borne in mind throughout the discussion that, in the most primitive vertebrate known, the epiblast is *permanently* single-layered. Into the peculiar method of the formation of the cerebro-spinal axis we need not enter.

(2.) In the Lamprey the epiblast does not divide until very late; in fact, not before the embryo has for some time been hatched (see Calberla, loc. cit., p. 264). This change takes place, however, in the region of the spinal cord before that organ has been formed, just as is the case in Amphioxus. The development of the nervous axis presents some peculiarities of a secondary nature. The sense organs are formed from the undivided epiblast.

(3.) The epiblast in the Elasmobranch Fishes separates into two layers much earlier than it does in the Lamprey, but still comparatively late in embryonic life, some time after the medullary canal has been completely closed, and several of the visceral clefts have appeared. According to Mr. Balfour it takes place at a stage slightly younger than K. The two layers are at first composed of flattened cells, but those of the inner stratum soon become columnar. "*Both layers apparently enter into the formation of the organs of sense.*"

(4.) In Triton the epiblast, though at first single, divides into its two parts at a very early stage, some time before the closing of the medullary canal (Stage c). When once formed the mucous layer becomes the active one and enters almost exclusively into the formation of the sense organs. So far as we are aware this is the only case as yet known in which there is a primitively single epiblast dividing early and delegating all its activity to one layer. It shows an approximation to the state of things found in the Frog.

(5.) In the Batrachia this is carried one step further and the two layers are distinguishable from the very first, even the roof of the segmentation cavity being double. The mucous or nervous layer, as in the Newt, enters alone into the formation of the organs of sense, &c. In short, almost the only difference in the matter of epiblast between the two classes of Amphibia lies in the *time* of its division.

Now, we are very far from asserting that these forms we have been considering represent the line of descent of the Batrachia; but we are decidedly of the opinion that they exhibit the steps of the process by which the epiblast of that group has reached its present complication. For

this reason we are forced to the conclusion that even the early condition of the epiblast in the Batrachia is a secondary modification, and *that the primitive condition of the layer is single.*

As opposed to this conclusion may be adduced the fact that in the spinal cord of the Batrachia the two layers at first fuse together and at a later time reappear, as if the double-layered condition were a primary, the single-layered a secondary, and the reappearing double layer a tertiary stage in development. And further, that the first stage has been retained only in the Batrachia and (?) Osseous Fishes, and lost in other known vertebrates. But this appears unlikely, and standing entirely by itself, the above-mentioned fact cannot be considered to have any great value.

The Hypoblast.

We shall now continue the history of the hypoblast from Stage A onwards, until the development of the notochord. The embryo at this stage (see Pl. XX, fig. 4) is still spherical. In the section figured, which is in the anterior region of the embyro, the alimentary canal is broad and low, lined above by a deep single layer of columnar hypoblast cells. These are broader and longer than the epiblast cells above them, with nuclei of a spherical rather than oval shape. They are in contact with the epiblast broadly across the middle line, but at the sides, just below the two slight folds on either side of the medullary groove, the mesoblast begins to intervene as a single layer of small cells. Beneath these the hypoblast cells lose their columnar shape, and becoming more quadrate are gradually reflected around the sides of the alimentary canal, becoming continuous on the one hand with the quadrate yolk cells lining the alimentary canal below, on the other with the cells bounding the great mass of yolk. This continuity has been carefully represented in Pl. XX, fig. 4. Where the invagination cells cease would be difficult to state, owing to the fact that the bending down at the sides is a gradual process partly dependent upon the growth of the mesoblast.

The hypoblast can now be classed according to its development under two heads. (*a.*) The cells above the alimentary canal, which have arisen from invagination and are continuous with the reflected epiblast at the blastopore. This we shall call the invagination hypoblast. (*b.*) Those cells lining the alimentary canal below and those immediately bounding the yolk elsewhere, which arise by histological

changes in the yolk cells proper. We shall refer to this as the yolk hypoblast.

The growth of the former class has been already considered in full. The latter arises by a slow process of metamorphosis in the peripheral yolk cells. The changes are not difficult to follow. The square yolk cells split as they approach the surface into long columnar or oblong cells, and at the same time a change takes place in the yolk spherules with which they are loaded, so that they show a greater avidity for the staining fluid. The large spherical nuclei of the yolk cells give place to the characteristic oval nuclei of the hypoblast. These primitive hypoblast cells assume more regular proportions as development proceeds. In the splitting off of the mesoblast which soon follows, fresh cells are constantly supplied from the yolk.

A further notice of Calberla's[1] views upon these points will perhaps not be out of place here. He considered the Lamprey embryo immediately after invagination to consist of two layers, the primary entoderm and the ectoderm. The former divides everywhere, except across the axial line, into the secondary entoderm and the mesoderm. Across the axial line the primary entoderm remains intact. He does not admit that the mesoderm arises even in part by invagination; but, still more important as it bears on the question under discussion, he does not include the outer yolk cells as part of the primary entoderm. So what we shall consider hereafter as the lateral mesoblast, he concluded, was joint mesoblast and hypoblast, not allowing that the outer yolk cells formed a distinct layer. The comparison has been inserted because at this period of its history the Lamprey presents many points in common with the Newt.

To resume the study of the hypoblast in Triton, it may be considered in the latter part of Stage c as forming a continuous layer around the yolk and completely enclosing the alimentary canal. By Stage n a very decided change has taken place (see Pl. XX, fig. 5) The section is in the head region where the alimentary tract has now reached a considerable size. The hypoblast is now only in contact with the epiblast in the median line, although the connection is such a close one that the three or four cells, still adhering, impinge so closely as to form a decided indentation in the epiblast—a feature which has been previously noticed in the Elasmobranch Fishes. The middle cells have also elongated and narrowed considerably, while those at the sides remain shorter; this results in a rounded upper outline. Laterally,

[1] *Vide* E. Calberla, loc. cit., on '*Petromyzon planeri*.'

they are still markedly continuous with the yolk hypoblast cells lining the alimentary canal and their lower margin arches upwards so as to form part of the lumen of the canal. This bending around of the hypoblast, which in Stage A was almost a straight line, into an arch of cells, must be partly attributed to a mechanical cause, viz. the rapid ingrowth of the mesoblast plates. Whatever the exact cause of this change it is well to note that no vital alteration has as yet taken place—the change is one merely of position. Elsewhere the hypoblast shows no new features.

Inasmuch as the interest in the hypoblast chiefly centres around the development of the notochord we shall consider the history of that organ by itself and complete the hypoblast later.

The Mesoblast.

It is evident from transverse sections in the latter part of Stage A (see Pl. XX, fig. 4) that the lateral plates of mesoblast have already attained a considerable thickness. At the junction of the invagination with the yolk hypoblast they are three or four cells deep, thinning out rapidly at the sides. In the anterior sections they barely extend below the middle, while behind they meet as a single layer of cells at the bottom, thus encircling the hypoblast except in the axial line above.

The lateral downward growth of the mesoblast in Triton is plainly not from the epiblast, for the epiblast has by this time formed a distinctly bounded single layer. There remain two modes in which it may *in great part* arise, (*a*) from the hypoblast; (*b*) independently of the hypoblast, from the yolk. This is of course excluding the mesoblast in the region of the alimentary canal which accompanies the process of invagination. If we consider, as we have reason to do from the analogy of the Frog, that the cells bounding the yolk form the primitive yolk hypoblast layer, we can only accept the former hypothesis. In the anterior section of Stage A the cells bounding the yolk below are as unquestionably hypoblastic as those bounding it above and at the sides. In other words, the hypoblast has formed as a distinct layer in contact with the epiblast below, before the mesoblast has appeared below at all. Moreover, at the sides, the down growth of the mesoblast is preceded plainly by a splitting off of the outer portion of the yolk hypoblast into large quadrate cells, and these in turn are seen in the process of subdivision. Although this growth seems to be at the expense of the hypoblast, it cannot be considered to arise altogether independently of the *down-*

growth of the invagination plates by a process of cell division, for the mesoblast does not arise at separate points, capping the hypoblast, but in direct continuity with the invagination mesoblast.

In the Elasmobranch Fishes, in which the origin of the mesoblast has been carefully observed, there is no doubt that this layer arises as two lateral masses, splitting off from the hypoblast at the same time that the latter arises as a distinct stratum from the lower layer cells. Here, however, the lateral plates do not form a continuous layer with the mesoblast which occasionally arises at the reflection of the epiblast at the sides, but are distinct from it.

Calberla,[1] as previously stated, explains the growth of the mesoderm (mesoblast) in the Lamprey, as an early splitting of the outer portion of the primary endoterm. This view fully confirms our interpretation of the lateral growth in Triton.

In Kowalevsky's earlier researches upon Amphioxus he fell into the error of supposing the mesoblast of double origin, hypoblastic and epiblastic, an error which he corrected later[2] by attributing this layer to a constriction off from the hypoblast, which occurs subsequent to the formation of the notochord. The simple invagination does not give rise to any but the two primitive layers. There can now be no doubt that the formation of the mesoblast is in all types a secondary phenomenon which is retarded in the simpler forms, and hastened in the more complex into an earlier period of development.

To review the features noticed in Stage A. The mesoblast arises by invagination as two lateral plates, and is never found across the median line. Subsequent growth is partly by cell division of these plates; mostly, however, at the expense of the hypoblast. The most rapid development is posteriorly, both in respect to thickness and downward growth. There is no tendency to split into somatic and splanchnic layers. By Stage B the mesoblast shows a very marked progress. It is now thickest immediately below the medullary plates, and causes that upward curve in the outline of the epiblast previously mentioned (Plate XX, fig. 5). At the same time the lateral plates have approached each other, bending the hypoblast downwards, so that now it is continuous with the epiblast only in the median line. The section figured is in the anterior part of the embryo near the head region. The cells appear larger than in the last stage,

[1] E. Calberla, loc. cit.

[2] *Vide* A. Kowalevsky, 'Archiv. fur Micros. Anatomie.' Band 13, p. 191.

near the axial line they are crowded together irregularly, but at either side the splitting into two single-celled layers begins to be evident. This splitting begins anteriorly and proceeds slowly backwards. In the posterior sections of the same embryo it is barely evident, although the cells show a tendency to arrange themselves in two rows. Plate XX, fig. 6, represents a section from the trunk region during Stage C, and shows that the splitting of the mesoblast extends slowly backwards. In this region the layer is now thinner than it is forwards, although the reverse of this is true of Stage A, where the mesoblast is thickest posteriorly. The proximal cells now begin to arrange themselves radially around the vertebral portion of the future body cavity, closely impinging against the epiblast, and tending to grow in above the primitive notochord. The body cavity does not extend beyond the medullary folds in this embryo, for here the two rows of cells suddenly terminate in a single row bending around the sides. In other respects the mesoblast shows no new features until Stage D. Sections of an embryo, during the latter part of Stage D, show that the neural canal has completely closed. The section figured in Plate XX, fig. 7, is in the anterior trunk region, here the mesoblast appears as two great triangular muscle plates, expanding above so as to fill the space formed by the fusion of the medullary canal, and enclosing the large body cavity. The two layers now extend completely around the embryo, but have not separated except in the upper region. In Stage F the division into somites has begun.

To conclude, there is one feature in the development of the mesoblast, which argues strongly for the fact that, mesoblastic invagination being begun, lateral growth sets in at once; that is, the cells formed by invagination are immediately supplemented by those growing down at the sides, of hypoblastic (yolk cell) origin. As evidence of this we find the mesoblast of the posterior sections meeting in the median line below, before it even reaches the ventral region anteriorly. In this single respect, the mesoblast develops more rapidly behind than in front. Subsequent to the formation of the alimentary canal, the greater energy of the embryo is directed to the head region, and all following growth is from before backwards. This is true of the thickening of the lateral plates, of the splitting into two layers, of the formation of the body cavity, and of the subsequent division into somites.

The Notochord.

In our description of the hypoblast, we considered the layer as classed under two heads, the invagination hypoblast, and the yolk hypoblast; it is with the former that the development of the notochord is concerned. The cells lying during Stage B between the mesoblast plates may be considered the primitive notochordal cells.

The first indication of the growth of the notochord in Triton (see Plate XX, fig. 5), is the tendency of the cells to take a radiated arrangement. We may now at the outset, point out three prominent features. First, the hypoblast consists of a single layer of columnar cells running from the epiblast above to the alimentary canal below. Second, these cells may be identified with the broad band of invagination cells which in Stage A were all in contact with the epiblast. They have been bent down by the ingrowth of the mesoblast above. Third, these cells are directly continuous at the sides with the yolk hypoblast.

In the Lamprey,[1] *Petromyzon planeri*, the relations of the hypoblast at this point to the epiblast and mesoblast are practically the same. There is the same close and broad contact with the epiblast, and the cells are of the same relative size. Here, as in Triton, the primary or invagination cells are alone concerned in the origin of the notochord.

In the Frog (*Rana temporaria*)[2] the primitive condition of the notochord is a great cubical mass of small cells, confluent with the epiblast above, and with the mesoblast at the sides. These do not all enter into the formation of the notochord, however, for at the time this organ begins to be constricted off, the lower cells form a hypoblastic lining to the alimentary canal. Götte's account of the first appearance of the notochord in the Frog (*Bombinator igneus*) differs widely, owing to the fact that he has mistaken the upper hypoblast cells for the mesoblast.

In the Elasmobranch Fishes[3] the arrangement is analogous, for the whole layer with the exception of a thin line of cells over the alimentary canal, enters into the notochord. The cells are at no time so widely in contact with the epiblast as in Triton; so the change preceding the formation of the notochord consists, first, in the lengthening, and then splitting of the cells into two lines placed end to end. The lower line thus formed is, however, mostly absorbed in the

[1] *Vide* E. Calberla, loc. cit.
[2] *Vide* E. Calberla, loc. cit., p. 260.
[3] *Vide* Balfour, loc. cit., p. 93.

formation of the organ, and is not, as in *Rana temporaria*, wholly expended in forming the upper layer of the alimentary canal. To return to Triton, it is well to notice here that the upper boundary of the alimentary canal is formed by the cells which will give rise to the notochord, and that the latter at this period actually contains part of the lumen of the canal.

Following the notochord into the succeeding stage, we find no marked changes (Pl. XX, fig. 6). The section taken from the middle region of the embryo presents much the same appearance. From this we infer that in common with the other organs, the notochord develops more rapidly forwards, and that the backward development is a slow one, for in Stage C the notochord is but little more advanced in the middle region of the embryo than it is in the anterior region in the preceding stage. The primitive features pointed out above remain constant.

Unfortunately there is a gap in our sections here, at least we have none by which we can trace the histological changes from the simple fold of hypoblast cells in Stage C, to the firm rod of radiating cells in the latter part of Stage D. There is no evidence of their splitting into two cells deep previous to this result as in the Lamprey and the Elasmobranchs. The exact process beyond the ascertaining of this point is of little real importance.

In Stage D (Pl. XX, fig. 7) the relations of this organ are not much altered, it still impinges against the epiblast above, and partly bounds the alimentary canal below, but the continuity with the hypoblast has been broken off, and the line of demarcation is plainly marked by the different character of the cells. The notochordal cells are subquadrate in shape, about twelve in number in a transverse section, and are arranged around a centre of their own. In other words, the notochord is now an independent body; at its sides below are the long narrow hypoblast cells which partially enclose it, and above are the mesoblast plates fully formed, which, however, show no tendency to surround it.

The notochord is now larger than at any subsequent stage. In its formed or permanent condition, it persists as a close granular mass in which we can sometimes detect cell division, sometimes not. (See Pl. XXI, fig. 8; figs. 12 and 13.) In Stage E an ingrowth of hypoblast below, cuts off its connection with the alimentary canal. In a much later period, Stage M, it has a vacuolated appearance; a branching network of connective tissue supporting promi-

nent nuclei, an appearance which has been noticed in many other forms (Pl. XX, fig. 15).

This completes the interesting history of the development of the notochord. To summarise: The invagination hypoblast cells are first continuous as a single layer, wholly across the median line; those farthest from the three central cells are gradually pushed down by the ingrowth of the mesoblast. There is no tendency to split below. They are further reflected around until the lateral cells meet, and the continuity with the hypoblast is broken. It still impinges against the epiblast above, and forms the upper boundary of the alimentary canal below.

A comparison has already been instituted between the development of the notochord in Triton and its development in the Frog, the Lamprey, and the Elasmobranch Fishes. In important details the processes are very similar. To carry the comparison a step further, in Amphioxus the notochord is differentiated from the hypoblast before the mesoblast has become constricted off, and at the time that the medullary plate is closing in above.

Hensen has demonstrated, beyond doubt, that the notochord is of hypoblastic origin in the Guinea-pig; and that it probably arises in the same way in the Rabbit. Quite recently,[2] Mr. Balfour has shown that it has a similar derivation in the Lizard, *Lacerta muralis*.

In several respects the notochord arises in a simpler manner in Triton than in any of those forms in which the process has been clearly followed out. In that: first, the cells do not reduplicate vertically, as in the Elasmobranchs and the Lamprey, previous to the formation of the organ; second, when the organ is completely formed, it still bounds the alimentary canal below, as in neither of the other forms nor in the Frog; third, no portion splits off subsequently to form the hypoblast layer bounding the canal above, this layer appears from the sides.

It is difficult to judge from Kowalevsky's description, whether the whole depth of the layer bounding the canal above is absorbed by the notochord, or whether the lower portion remains as an upper lining of the canal, and the upper portion alone enters into the notochord. If the latter is the case, the Newt presents the simplest notochordal development known.

The evidence from all these forms points so strongly in one direction, as to amount almost to proof, that the study

[1] *Vide* Kowalevsky, loc. cit.

[2] *Vide* F. M. Balfour, this Journal, Vol. XIX, p. 3, New Series.

of the more important types which have not as yet been observed, and the clearing up of the doubts which still envelop other types, will fix the derivation of the notochord from the hypoblast as a law, rather than as a feature positive in some cases, and with an exceptional origin from the mesoblast in others.

The Hypoblast.

In Stage C the notochordal cells are continuous at the sides, with the layer of hypoblast lining the yolk (see Pl. XX, fig. 6). In Stage D this continuity is completely broken, the layer appears as a long narrow row of cells, flattened against the sides of the notochord, but not enclosing it below. Elsewhere this layer shows no new features. In Stage E, however (see Pl. XXI, fig. 8), the cells have grown down and meet below, completely surrounding the alimentary canal and shutting it off from the notochord. This process is interesting, as it shows that, while the original upper lining is mainly absorbed by the notochord, the permanent upper lining is formed from the yolk hypoblast cells, and that now almost the entire layer is formed of this secondary hypoblast, the bulk of the primary or invagination hypoblast having gone to the notochord. The hypoblast grows under the notochord, in much the same way in the Lamprey, but at a somewhat earlier stage. In most of the other forms there remains throughout, a thin layer of cells intervening between the notochord and the yolk.

Body Cavity and Somites of the Head.

As already mentioned, the growth of the mesoblast is from behind forward, and in Stage A (Pl. XX, fig. 4) we see that in the head region the mesoblastic plates do not meet ventrally. They gradually thin out forwards and end near the blind termination of the alimentary canal. At this period the mesoblast is quite thick, and is composed of numerous cells of spherical shape, but exhibits no tendency to become divided into somatic and splanchnic layers. In Stage B, however, the cells have arranged themselves into two layers, and quite a cavity has appeared between them (Pl. XX, fig. 5). As yet this change is confined to the head, and so there is a cavity in the head on each side of the middle line, contained between the somatic and splanchnic layers of the mesoblast. These cavities, therefore, are parts of the pleuro-peritoneal cavity, and when that is formed in the body, will be directly continuous with them. As in the

Elasmobranch Fishes,[1] the cavity in the head is formed at a period considerably before that at which it appears in the body. These two *head cavities* have no communication with each other, as the mesoblast in the head is in two separate masses. A longitudinal horizontal section (Pl. XXI, fig. 10) through an embryo slightly older than F shows this cavity (*pp.*) as an undivided slit bounded by columnar mesoblast cells. But when the first visceral cleft appears as an outgrowth from the hypoblast of the throat to join the external skin, this cavity is necessarily separated into two portions, one behind and one in front of the cleft. This cleft in the latest stages we have been able to observe never pierces the skin, but it lies close to it and so divides the mesoblast. The second cleft divides the cavity into three sections, and each succeeding one adds a fresh segment to the number. Of course this number is not so great as it is in the Elasmobranch Fishes.

The section in front of the first cleft presents some features which demand attention. It grows forward and becomes divided spontaneously into two portions, one of which lies close to the optic vesicle (Pl. XXI, fig. 11), and entirely in front of the mouth, while the second (2 *pp.*) is enclosed altogether in the mandibular arch. The first aortic arch (1*aa*) runs between these two sections and somewhat dorsal to them. We have not been able to make any satisfactory observations upon their relation to the branches of the fifth nerve, but from their position it seems in every way probable that they have much the same relations as those described by Mr. Balfour in the Elasmobranch Fishes. The first division shows a small lumen surrounded by a layer of short columnar cells; in longitudinal vertical sections (Pl. XXI, fig. 11, 1 *pp.*), it has a somewhat oval shape; in transverse sections (fig. 13, *pp.*) it has a transversally elongated shape, and the cavity in these sections is seen to be largest toward the middle line. During no period as late as Stage L could we find any trace of a ventral union between the anterior segments of each side, such as occurs in the Elasmobranchs. It may, however, occur later, as during Stage L they approach very closely. The second segment (Pl. XXI, fig. 11, 2 *pp.*) is considerably smaller than the first, and has a very small lumen. Its cavity also is lined with columnar cells, and forms a narrow slit running parallel to the first visceral cleft. The mandibular aortic arch lies just anterior to it instead of close to its inner side as in the Elasmobranchs. The other segments of the head cavity lie in the visceral

[1] Balfour, loc. cit., p. 86.

arches, and show narrow cavities lined by columnar epithelium (Pl. XXI, fig. 12, 3 *pp*). They present no features of especial importance. We have not followed out the subsequent development of these segments, but in all probability their cells become transformed into muscle cells.

In the foregoing description there will be observed a very close similarity to what has been described for the Elasmobranchs; in fact, with some minor exceptions, and the one important one of the non-communication of the first pair of segments, Mr. Balfour's descriptions will apply equally well to our specimens. This is of the more interest, for Triton in this respect is very much more like the Elasmobranchs than it is like the Batrachians; a fact which is somewhat remarkable. In the Batrachians so carefully investigated by Dr. Götte,[1] there appears to be no head cavity formed at any period. On the other hand, two series of segments, an inner and an outer series, become formed, and are believed by Dr. Götte to correspond respectively to the vertebral and lateral plates of mesoblast which are developed in the trunk. The internal segments resemble the protovertebræ in shape, but are smaller; their walls develop into muscular fibres and represent the anterior continuation of the dorsal muscles. The external segments are contained in the visceral arches. In the anterior division of the head (Götte's Vorderkopf) there is only one pair of segments, as the division of the segment in front of the first visceral cleft does not seem to occur; the part contained in the mandibular arch is derived from the growth of the postero-lateral segments. The most anterior segment of all gives rise, as in the Elasmobranchs, to the muscles of the eye.

It is remarkable how very different all this is from the process observable in Triton. There are found in the posterior part of the head four segments which give rise to muscular fibres, as in Bombinator, and continue the dorsal muscle forwards. These may be equivalent to the four internal segments of the head of Bombinator, but they have no ventral continuations. They are more to be compared with segments in the posterior part of the head of the Elasmobranchs. With regard to the latter, Mr. Balfour says, (p. 209), "All my efforts have hitherto failed to demonstrate any segmentation in the mesoblast of the head other than that indicated by the sections of the body-cavity before mentioned, but since these must be regarded as equivalent to muscle plates any further segmentation of mesoblast could not be anticipated; to this statement the posterior part of the

[1] Unke, pp. 203-208, 216-229.

head forms an apparent exception. Not far behind the auditory involution, there are visible at the end of Period K a few longitudinal muscles, forming about three or four muscle plates, the ventral part of which is wanting. I have not the means of deciding whether they properly belong to the head or may not be a part of the trunk system of muscles which has to a certain extent overlapped the back of the head, but am inclined to accept the latter view." The appearances here described are very much like those to be seen in Triton, and we are not in a position to pronounce any more decided judgment upon them, than upon those of the Elasmobranchs; but taking into consideration Götte's figures we are rather inclined to consider them the axial segments of which the plate containing the head cavity is the lateral part. The chief differences between the two types of Amphibians lie in the cavities themselves, and the number of segments in the anterior part of the head.

Our researches do not, we regret to say, throw much new light upon that difficult morphological problem, the segmentation of the head. It is interesting to find that as in the Elasmobranchs there is one præ-oral segment, as might be expected to be the case if the head cavities afford any trustworthy guide to the number of head segments. Of course the number of postoral cavities is less than in the Elasmobranchs owing to the fewer gill clefts, but this is a feature which does not affect the question at issue.

Of whatever value these facts in the development of the Newt are considered, we think that they favour the views expressed by Mr. Balfour in p. 216 of his book. For these head cavities, if of morphological importance, might be anticipated to be fairly constant in character.

The Thyroid Body.

Pl. XXI, fig. 12, represents the earliest condition of the thyroid body which has fallen under our observation. In it we see that in the region of the mandibular arch there is a *solid* outgrowth of cells from the ventral wall of the alimentary cavity which has reached the inner layer of the epiblast. The latter has at the point of contact risen up slightly from the external layer leaving a small triangular space between them. In the next stage (fig. 13), the inner layer of epiblast has coalesced with the hypoblastic outgrowth and is discontinuous across the middle line. It is now difficult to determine where one layer begins and the other ends, so

complete is their fusion. The external layer is never interrupted. Fig. 14 presents a rounded thickening of the fused mass, which is the next step in development.

The latest stage we have (somewhat later than M) shows the gland separated from the epiblast (Pl. XXI, fig. 15) which is now continuous across the middle line, but still connected with the ventral wall of the œsophagus by a cord of cells. The thyroid is now a solid cylindrical rod of considerable length, ending posteriorly near the ventral aorta; the section shows an aortic arch (1 *aa*) cut through longitudinally. The gland consists of an outer or cortical layer of columnar cells arranged radially, and an inner small kernel of rounded cells. As yet there is no trace of a lumen, or any division into lobules. Further than this we have not been able to follow its development, but have no reason to suppose that it presents any great peculiarities.

On the whole the thyroid body of the Newt corresponds quite closely in position and mode of development to the same body in the Elasmobranch Fishes; but there are some points of difference to which we should like to call particular attention. (1.) In the latter the diverticulum of the hypoblast is hollow in front and solid behind at first, and only subsequently becomes solid throughout, while in Triton we have not been able to discover any stage which shows a hollow outgrowth. The solidity, however, does not occur from any confused mass of cells, but from the fact that the two sides of the diverticulum are pressed closely together (Pl. XXI, figs. 12 and 13). Of course it is very possible that we have missed a stage in which the outgrowth was hollow; but if that is the case that condition must be a very transitory one. The difference is only one of detail in any case. (2.) Of much more importance is the fact that in the Elasmobranchs there is never found any indication of continuity between the hypoblast and epiblast, which at this period is still single layered. But the diverticulum is pressed very closely against the epiblast, presenting just the appearance of the first visceral cleft which does not perforate the skin.[1] (We do not wish to intimate by this comparison an opinion that the thyroid is a modified visceral cleft, because all diverticula from the throat to the external skin must look more or less alike.)

The account given by Dr. Götte[2] of the development of the thyroid in Bombinator is still more like our account than is that given by Mr. Balfour of the Elasmobranchs.

[1] Balfour, loc. cit., Plate XIV, fig. 5*a*, p. 223-5.
[2] Loc. cit., p. 667.

In Bombinator the thyroid "is formed from a pit of the hypoblast, which persists as the remains of an early depression of the hypoblast behind the mandibular arch, *produced by a fusion of the epiblast and hypoblast*" (Taf. viii, fig. 127-130, and Taf. xiii, xv, xvi, figs. 292 and 293.) At first it is connected anteriorly with the median division line which bisects that arch; after the disappearance of this the rudiment of the thyroid appears as a funnel-shaped diverticulum of the hypoblast and is free behind. The fusion between the two layers, which in Triton persists for a considerable period and is seen throughout the length of the gland, here is confined to the anterior end, and remains only a short time.

W. Müller, in his account of the development of the thyroid body[1] in *Rana temporaria*, does not give any figures or descriptions leading us to suppose that he has observed this continuity of the layers.

We must confess that we ourselves are very much puzzled by the fusion of the epiblast and hypoblast at this point, and are unable to give any morphological explanation of its meaning. Is it not just possible that it may represent some shifting in the position of the mouth? but if so, we shall be obliged to abandon, for this form at least, the homology of the thyroid body with the endostyle of the Ascidians. We mention it with the hope of directing the attention of some morphologist, who will clear the matter up, to this curious and unexplained feature.

It may be of use to give a brief summary of the points which we have endeavoured to establish in this paper, before passing on to consider to what general conclusions these points lead us, if established.

1. As to *external features*, we have failed to find in Triton the suckers and horny teeth with which the Batrachian larva is furnished.

2. *Segmentation* proceeds in a manner much like that of the Frog, but the roof of the segmentation cavity is from the very first only one cell thick.

3. *An unsymmetrical invagination*, like that of the Frog and Lamprey, takes place, giving rise to one layer in the middle line, the hypoblast, and two at the sides, hypoblast and mesoblast. The invagination mesoblast is supplemented by other cells, which split off from the yolk hypoblast. These two lateral and disconnected masses of mesoblast are, we consider, the homologues of the paired hypoblastic diverticula in Amphioxus.

4. The *epiblast* is at first composed of a single layer of

[1] Jenaische, 'Zeitschrift,' 1871, pp. 435-439.

columnar cells, which early separate into two rows, and of the two layers thus formed the inner becomes the active one, entering exclusively into the formation of the sense organs. In the spinal cord and brain the division into two layers does not take place till very much later.

5. The *hypoblast* is of two kinds, the invaginated and that which arises from the metamorphosed yolk-cells.

6. The *notochord* is of hypoblastic origin, and takes up the entire dorsal wall of the alimentary tract (except in the head) in its formation, fresh hypoblast growing from the sides below it. It becomes well formed and cylindrical in shape before any cell division takes place in it.

7. The *body-cavity* extends into the head, appearing in this region first. The head mesoblast becomes split into somites, which have the same relations and number (except so far as modified by the reduction of the visceral clefts) as in the Elasmobranchs, but do not seem to communicate below.

8. The *thyroid* body is formed by an outgrowth from the alimentary canal, the walls of which become continuous with the mucous layer of the epiblast; the continuity of the horny layer is not interrupted.

Conclusion.

If the statements in this paper prove to be well founded, they will give us some data for judging of the relationships of the two groups of Amphibia to each other, and to some lower types. The marked divergences from the Batrachian type which the Newt shows us point to the conclusion that the Urodeles and Batrachians have been separated for a very long period. And it is interesting to observe that, in those cases where the divergence is other than a mere matter of detail, it leads towards the Lamprey, and through that to Amphioxus. The opinion seems to be gaining ground that some such form as the Lamprey is the point toward which the Amphibia, the Elasmobranch, Ganoid, and Dipnoic fishes converge, and the more these types are investigated the better established appears this view. As yet, however, we are not in a position to pronounce upon it with even an approximation to certainty. The observations brought forward in this paper tend strongly, we think, in this direction, and we hope that future investigations upon the Amphibia, the Ganoids, and especially the Dipnoi, will soon put the matter to a crucial test.

In conclusion, we must express our very sincere thanks to Mr. F. M. Balfour for his never-failing kindness and assistance to us while engaged in this work.

The Structure *of* Haliphysema Tumanowiczii. By E. Ray Lankester, F.R.S. (With Plate XXII.)

A remarkable dispute has been carried on during the past year concerning a minute marine organism which forms a tubular case in shape like a "cornucopia," scarcely so large as a letter "y" as printed on this page. These little tubes were first described by Dr. Bowerbank (in 1864, 'British Spongiadæ,' Ray Society), and were considered by him to be the skeletons of a very simple kind of sponge, to which he gave the name Haliphysema. Two species were described by that author, viz. *H. Tumanowiczii* and *H. ramulosum*. Mr. Carter, in 1870 ('Ann. and Mag. Nat. Hist.,' p. 309) brought forward reasons for considering these little tubes as the work of quite another group of organisms, viz. the Foraminifera, and described what he considered as a closely allied form under the name "*Squamulina scopula*." In 1877 Professor Ernst Haeckel published in the 'Jenaische Zeitschrift' an account of Haliphysema, in which he recognised five species; with this genus he associated a new one, Gastrophysema, into which he placed the "*Squamulina scopula*" of Carter, and a new species *G. dithalamium*.

The soft parts of the Haliphysema of Bowerbank and of Carter's similar organism had never been described before Professor Haeckel's memoir on the subject. Haliphysema was simply known as a funnel-like shell of minute size, the substance of the shell being made up of particles foreign to the organism itself, namely, grains of quartz, spicules of sponges,—and any other such material. There was nothing in the structure of the tests of these organisms to forbid their association with the arenaceous Foraminifera or similar building forms of Protozoa. On the other hand, it was possible that they were the work of a sponge, a polyp, or even of a worm. Professor Haeckel gave a most minute and fully illustrated description, not only of the test of Haliphysema and Gastrophysema, but also of their soft living substance. His memoir is illustrated by three plates, and on these plates are figured, with ideal symmetry and precision, the appearance of these forms as seen when longitudinally divided in the living state. Professor Haeckel described Haliphysema and Gastrophysema as hollow mouth-bearing sacs, built of two layers of cells—an outer "syncytium" the ectoderm—and an inner closely set lining of flagellate "collared-cells," similar to those found in the ciliate chambers

of sponges. Further, he described and figured a number of egg-like bodies as adhering to the endoderm and formed by a modification of its cells. These were regarded as ova. Excepting for the absence of pores in the body-wall, the structure thus described corresponded very closely with that of the simplest examples of the Porifera or Sponges. In consideration of their wanting the pores characteristic of Sponges, Professor Haeckel proposed to place the genus Haliphysema of Bowerbank and his own new genus Gastrophysema in a new great group of Cœlenteric animals, to which he gave the name "Physemaria." The Physemaria were stated to represent the simplest two-cell-layered forms of life from which all the Metazoa (or Enterozoa) have been derived.

As such the Physemaria have been admitted into text-books (*e.g.* Gegenbaur's 'Grundriss'), and have formed the subject of many a discourse when the principles of phylogeny and the germ-layer theory have been expounded to zoological students.

Quite recently a doubt has been raised as to whether the "Physemaria" as a group have any existence at all. We are, in fact, asked to believe that *there are two sets of organisms exactly alike* in the details of their external structure, viz. the cornucopia-like tube with its disc-like base and its constituent spicules, &c., but differing from one another in the structure of their soft parts—the one being Protozoa, the other sponge-like multicellular Cœlenterates.

The matter has been brought to this pass by a series of papers in the 'Annals and Mag. of Nat. History,' contributed during the past year by Mr. Carter, the Rev. A. M. Norman and Mr. Savile Kent, and the difficulty of the position will be in no way diminished by the observations which I have myself made and am about to record. Mr. Carter, the original discoverer of Haeckel's *Gastrophysema scopula*, protests that the *chambered* nature of the shell of his little organism, and the extrusion of protoplasm in the form of pseudopodia from broken but living specimens, proves them to be Foraminifera and not Cœlentera. At the same time Mr. Carter is not able to state from observation that his specimens are devoid of an axial cavity lined by flagellate collar-cells.

Mr. Norman, on the other hand, after examining Mr. Carter's specimens of *Gastrophysema* (= *Squamulina*) *scopula*, and comparing them with Dr. Bowerbank's type-specimens of Haliphysema, and with other specimens and supposed diverse species of that genus, comes to the con-

clusion that all these forms, Gastrophysema and Haliphysema, *are but variations of one species*, necessarily referable to the original *Haliphysema Tumanowiczii*.

At the same time Mr. Norman has no observations to offer relative to the internal structure of the soft living animal, and accepts (as all zoologists would gladly do at this moment) Professor Haeckel's description as correct. Accordingly Mr. Norman refers Haliphysema to the Sponges.

In July, 1878, however, the 'Annals' contained a very important paper by Mr. Saville Kent. Whilst other zoologists had settled down to a belief in the Physemaria, Mr. Kent had not rested content till he obtained living specimens of these forms. These he procured in abundance at Jersey, and was now able to offer some most astonishing observations on Haliphysema. He figured in a drawing, which must be accepted as an accurate representation of fact, a specimen of the tube of Haliphysema, from which was issuing an abundant reticular protoplasm, spreading its filaments far beyond the tube, even to a distance of five times its greatest diameter ('Annals and Mag. Nat. History,' ser. v, vol ii, pl. v). This drawing represents, Mr. Kent tells us, what he saw of a living specimen examined intact on the field of the microscope.

The conclusion which Mr. Kent drew from this observation was perfectly legitimate. He concluded that he had before him a Reticularian Rhizopod. Further, he had no reason to doubt, especially after Mr. Norman's discussion of the subject, that the tube from which the protoplasm issued was that of Haliphysema (alias Squamulina, alias Gastrophysema). Accordingly, Haliphysema was shown not to be a two-cell-layered organism, but an arenaceous Foraminifer, one of Dr. Carpenter's Lituolida.

At the same time Mr. Kent is careful to point out that, should there be organisms, as represented by Professor Haeckel, corresponding to the forms identified by himself (Mr. Kent) with Haliphysema, and having internal cavities lined with collar-bearing flagellate cells, their sponge nature would be unquestionable, and we should have in them merely *remarkable isomorphs or external facsimiles of the Foraminiferal type*.

Being deeply interested in this controversy, and not knowing whom to credit nor how to explain discrepancies, doubting very much the "isomorph" theory, I applied to Mr. Saville Kent for living specimens of his *Haliphysema Tumanowiczii*.

With my request he most courteously complied, and sent

From Jersey, not only a quantity of living specimens, but subsequently others, carefully treated by reagents on the spot according to my directions.

I may confess, without offence to Mr. Kent, that I was intent upon discovering in his Haliphysema evidence of the syncytium and collar-bearing flagellate cells described by Haeckel, which, I thought it possible, might have escaped his observation. My inquiries were made on both living and preserved specimens, and have led to the discovery of a very interesting structure, which might at first sight be taken to indicate that the organism was built up of many cells, and was similar to a sponge. The structure, as described below, is, however, essentially that of the Protozoa, and leaves no doubt whatever in my mind that Haliphysema is to be referred to that group.

Whether there are isomorphs of Haliphysema constituting the group "Physemaria," as suggested by Mr. Kent, and as also asserted by Dr. R. Hertwig, of Jena, in Hoffman's and Schwalbe's 'Jahresbericht,' vol. vii, second part, is a matter which is clearly out of the field of discussion.

It is certainly most desirable that these "isomorphs" should be produced, as I earnestly hope that they will soon be, by my friend Profesor Haeckel, or else that some kind of explanation should be offered to remove the present puzzling antagonism of the statements which have been made in regard to Haliphysema and Gastrophysema, by Professor Haeckel on the one side, and by English observers on the other.

1. *Condition of the material studied.*—The specimens forwarded to me were in two conditions: firstly, several living specimens sent in a large vessel of sea water; secondly, specimens preserved in Jersey by Mr. Kent by placing them first in a large quantity—half a litre—of one sixth per cent. solution of chromic acid, from which, after a lapse of twenty-four hours, they were removed to strong alcohol.

2. *External test.*—In Pl. XXII, fig. 1, I have given a drawing of the external test of a small specimen, magnified 135 times linear. The specimens sent to me were very varied in form, some much more elongated than that figured; others with a more globose anterior region (like Gastrophysema); others exhibiting a nodose series of enlargements (polythalamous). The character and direction of the spicules and fragments of spicules used to form the test was not the same in all. The first specimens which I received *closely resembled* the Haliphysema figured by Haeckel in

the 'Jen. Zeitschrift,' but none were so perfectly symmetrical and uniform in the disposition of the spicules. It is, however, important to state that the forwardly-pointing spicules, giving the organism a brush-like appearance, are very nearly as abundant in *some* of the Jersey specimens as in Professor Haeckel's figure. The form which I have drawn was selected as being the commonest in the gathering sent to me.

There are certain very striking points of identity between the Jersey specimens and Professor Haeckel's figure. The first is the possession of a large disc-like or rather a hemispherical base, which gives support to a narrow stalk, comparable to the stem of a wine glass. The second is the composition of the test from sponge spicules, among which those of Reniera and Esperia predominate, associated with which are spicules of Calcispongiæ, fragments of the spines of Crustacea, and granules of quartz. It is obvious enough that a composite test of this kind is liable to vary in its components almost indefinitely, according to the material existing in its locality.

No pores or fenestræ are visible in the walls of the test, excepting anteriorly, where there is a considerable aperture in or deficiency of the test.

3. *The contents of the test.*—It is difficult to obtain from a fresh specimen of Haliphysema satisfactory evidence of the nature of the living substance which it encloses. Mr. Kent was fortunate enough to observe reticular protoplasm extruded from his specimens. Those which I received did not exhibit this phenomenon, owing, no doubt, to the fact that they had been affected by the journey. It was, however, possible, by carefully teazing the fresh specimens with needles, either in salt water or in osmic acid, to obtain fragments of a finely granular protoplasm interspersed among the broken-up spicules of the test. These fragments of protoplasm exhibited very usually one or sometimes three or four vesicular nuclei, which could readily be stained with picro-carmine. These nuclei were identical with those drawn in Pl. XXII, fig. 10.

The most successful method of separating the test from the contained soft matter I found to be the following:—Specimens which had been placed when quite fresh in chromic acid ($\frac{1}{6}$th per cent.), and, subsequently, in alcohol, were treated successively with absolute alcohol, oil of cloves, and Canada balsam, either with or without previous staining by hæmatoxylin. The whole specimen was mounted in balsam, and the covering glass then gently pressed, and moved

in such a way as to crack the test and roll away its fragments from the soft kernel within. In this way I succeeded in obtaining several more or less complete "cores" or "kernels," such as that figured in Pl. XXII, fig. 2.

These were sufficiently transparent to admit of their examination by the highest powers of the microscope, and by teazing stained specimens it was easy to obtain complete evidence of their structure.

The "core" of *Haliphysema*—I speak of the Jersey specimens, not of Professor Haeckel's—is a continuous mass of protoplasm, exhibiting no central cavity, and devoid of "cell-structure." On its surface this core is fluted and moulded to the shape of the adjoining spicule-fragments which form the test (see Pl. XXII, figs. 2 and 11 *r*). There appears to be no differentiation of a "cortical substance" on the surface of the core, though the protoplasm is more free from granules here than it is deeply.

The nuclei.—Scattered in the protoplasm are an immense number of vesicular bodies averaging $\frac{1}{1700}$th inch in diameter and of very constant size. These vesicular bodies stain deeply; their walls are thick and their contents finely granular or else hyaline. The wall of the vesicles stains much more deeply than their contents. In the living state these vesicular bodies are spherical in form; after the action of chromic acid or of alcohol they exhibit various conditions of collapse and shrinking; some of these are drawn in fig. 10. In teazed chromic-acid specimens the vesicles are readily isolated, frequently leaving a "bed" or space in the protoplasm from which they have been disinterred.

The term "vesicular nuclei" may be applied to these bodies which certainly constitute the most obvious structural feature of the soft substance of Haliphysema.

We have not to go far to find their parallel amongst the Protozoa. Though they differ in the fact that they are very abundant, and in their sharp emargination, from the nuclei recently discovered in Foraminifera by F. E. Schulze and Hertwig, yet it seems most probable that they are only an elaborated condition of such nuclei. In abundance and sharpness of outline they are paralleled or even surpassed by the vesicular nuclei of Pelomyxa, and it is also a conclusion admitting of little doubt that the peculiar oat-shaped corpuscles of Labyrinthula and Chlamydomyxa are further examples of the existence of very numerous sharply-defined nuclei existing in an organism which is, nevertheless, unicellular.

The vesicular nuclei which are now figured as character-

istic of Haliphysema occur in all probability in the other Arenaceous Foraminifera, and in other members of the group also. Dr. Carpenter figures in his classical monograph of the group, published by the Ray Society, certain vesicular bodies from *Orbitolites*, which correspond in size and general character with the vesicular nuclei of Haliphysema. It is, however, possible that the bodies found in Orbitolites are, as Mr. Moseley[1] has suggested, parasitic unicellular Algæ. Those of Haliphysema are certainly not parasitic, but integral parts of the organism in which they occur. In the fresh state they are colourless, whilst Mr. Moseley states that the corpuscles of Orbitolites are green when fresh (probably coloured by chlorophyll), and compares them with the yellow "cells" of Radiolaria, which have been supposed by Cienkowski to be parasitic.

Egg-like bodies.—The vesicular nuclei are most abundant in the basal portion of the core of Haliphysema. Anteriorly they are much diminished in number, and here I found in several specimens that the protoplasm was segmented into bodies of much larger size than the vesicular nuclei, varying from the $\frac{1}{1500}$th to the $\frac{1}{300}$th of an inch in diameter. These bodies correspond very closely with the "eggs" figured by Haeckel in his "isomorph" of Haliphysema.

The smallest of them (fig. 6) are devoid of nucleus, and the constituent protoplasm appears to be vacuolated. In the larger specimens the outline of the corpuscle is well defined, but there is nothing like a wall or capsular investment. The protoplasm has the rather coarsely granular character seen in egg-cells so usually, and a central nucleus is after some care to be made out. I obtained these bodies most satisfactorily for observation by teazing preserved specimens of the Haliphysema. One which I have figured is seen to be undergoing transverse fission. The formation of such egg-like germs within the general protoplasm of a unicellular Protozoon is entirely in accord with what is known as to the reproductive process in such organisms. There are numerous observations of long standing (see Carpenter's 'Foraminifera') which indicate such a formation of nucleated germs within the substance of the shell-bearing Reticularia, whilst the most recent observations on the Radiolaria confirm the earlier observation of a similar process in those allied forms.

The body substance in general.—The vesicular nuclei and the egg-like corpuscles are embedded in a finely granular

[1] 'Notes of a Naturalist on the Challenger,' p. 293.

protoplasm, which, when teazed and examined in small pieces, has the appearance of being built up by a meshwork of fine fibrillæ, or, to put it in another way, appears to consist of denser substance, honeycombed by very small "vacuoles" or spaces of less dense substance. Here and there are denser granules and small corpuscles, smaller and less emarginated than the vesicular nuclei.

In no part of the body substance is there evidence of any axial cavity comparable to the enteron of higher animals, nor the slightest trace of a breaking up of the protoplasm into areas or units corresponding to cells, with the exception of the egg-like bodies of the anterior region.

The external protoplasm.—In the specimens preserved in chromic acid, though no expanded networks of protoplasm, such as that seen by Mr. Kent in living examples, can be observed, having as a matter of course been retracted and shrunk during the disturbance preliminary to the action of the preserving fluid, yet in all my specimens knob-like masses of the protoplasm could be observed here and there on the *surface* of the unbroken tubes. The prettiest examples are those in which the protoplasm has been killed and preserved whilst crawling along the surface of one of the projecting spicules of the tube. In fig. 1 such knobs of protoplasm are seen, and in fig. 3 a camera lucida drawing is given of a spicule projecting well forward from the test of a Haliphysema, having on its surface a quantity of streaming (or rather what was streaming) protoplasm. An important fact is exhibited by this specimen, namely, that the vesicular nuclei pass out of the test and stream with the protoplasm over the surface of the spicules, and probably on to the network which is formed beyond in the living condition. One of the vesicular nuclei is seen in fig. 3 *n*.

From the preceding account it appears that the structure of Haliphysema is not quite so simple as that which has been supposed to characterise the body-substance of the Lituolida. It seems to me very possible that we shall eventually find among the larger members of the varied groups of organisms classed as "Foraminifera" as high a structural differentiation as that exhibited by any of the naked fresh-water forms of Gymnomyxa (Rhizopoda) such as Pelomyxa, Chlamydomyxa, and Actinosphærium. Possibly, when means are taken to overcome the difficulties of observation presented by their opaque and resisting shells, the larger "Foraminifera" may prove not only to be nucleated but to be as highly organised (though not in the same way) as the Radiolaria.

LITHAMŒBA DISCUS, nov. gen. et sp., *one of the* GYMNOMYXA.

By E. RAY LANKESTER, F.R.S. (With Plate XXIII.)

I INCLUDE under the division Gymnomyxa all those Protozoa or Homoblastic animals which expose, in a naked state, to the medium in which they live, the living protoplasm of their body-substance, in the form of those lobose, filamentous, or reticulate processes known as pseudopodia. The group is the complement of the Corticata, in which a permanent differentiation of the surface of the body-substance has been effected, necessitating either parasitic nutrition (Gregarinæ) or the specialization of an ingestive orifice (the Ciliate, Flagellate, and Suctorial Infusoria). The Gymnomyxa thus include, together with the Radiolaria and others, all those forms known as Rhizopoda, whether provided with nucleus or devoid of that structure.

In examining a gathering from a pond near Birmingham, forwarded to me in April last by Mr. Bolton of that town, I observed six specimens of an organism belonging to the group of the Gymnomyxa, apparently hitherto undescribed.

The organism in question is related to the Amœbæ, having the coarse, lobose pseudopodia characteristic of that genus. At the same time the protoplasm of which it consists is vacuolated in a remarkable way not observed in Amœba, and moreover, numerous peculiar concretions are embedded in its substance, which are not precisely like anything known in Amœba. The actual form of the processes of the body-substance or pseudopodia extruded by the present form is also not identical with that of the pseudopodia of the commoner Amœbæ, such as *A. princeps* or *A. radiosa*, but rather resembles the hernia-like extrusions of the protoplasm exhibited by that very remarkable example of the freshwater Gymnomyxa, *Pelomyxa*, described a few years since by Professor Greef, a form which I have had the good fortune to find also in this country.

The new Protozoon I propose to call *Lithamœba discus*, the generic name having reference to its characterstic concretions, and the specific name to the form which it assumes when in a quiescent condition.

I am not able to furnish any particulars as to the life-history of *Lithamœba discus*, but it appears to me that the details of its structure are sufficiently interesting to merit publication.

Form of the body.—In Plate XXIII, fig. 1, a specimen is

represented as seen in the living condition, quiescent. It consists of a discoid mass of protoplasm the $\frac{1}{115}$th of an inch in diameter.

The concretions.—The periphery of the disc is clear and colourless, towards the centre a dark greyish appearance is observed, owing to the large number of rounded concretions of a highly refringent substance which are embedded in the protoplasm. Most of these concretions are of minute size, with a tendency to a reniform shape. Two much larger concretions are seen, the larger of which measured the $\frac{1}{710}$th inch in length. The substance of which these concretions are formed was not determined. It resists the action of dilute acetic acid and of dilute caustic potash, but is dissolved by strong hydrochloric acid.

In fig. 8 one of these concretions is represented from another specimen isolated.

The nucleus.—A single nucleus (*n*), of large size, measuring $\frac{1}{500}$th inch in longest diameter is present. It has an irregular block-like form and a very obvious and definite structure. It is enclosed in a well-differentiated membrane, which can be separated from it by the action of reagents (fig. 5). Its substance appears to be built up by a number of minute, closely-set granules, which are angular and set side by side in a cementing substance. There is no specialised nucleolus, nor are nucleolar fibrillæ to be observed.

Food matters.—Besides the concretions and the nucleus the protoplasm contains a quantity of food débris (*ff*), consisting of a frustule of the Diatom Navicula, and the carapace of a Rotifer and other matters.

Contractile vacuole.—The centre of the disc is occupied by a very large vacuole (*cv*), containing a clear liquid, and having, both above and below, excessively thin walls. The vacuole measures $\frac{1}{310}$th inch in diameter. Continued observation showed this vacuole to be contractile, and that its contents are discharged periodically to the exterior.

Vacuolar structure of the protoplasm.—In focussing the upper wall of the vacuole I first became aware of the excessively fine reticulate or vacuolar structure which characterises the protoplasm of the whole body. This differentiation of the protoplasm can be detected all round the margin of the disc also, and, in fact, wherever the protoplasm is sufficiently free from concretions or food matter to allow of proper illumination and inspection. This vacuolar structure, as seen under a No. 10 immersion objective after treatment of a specimen of Lithamœba with osmic acid, followed by picro-carmine, is represented in fig. 4.

The staining with picro-carmine did not affect the concretions, but was taken very strongly by the whole contents of the nuclear cyst.

The cuticle.—Iodine was applied to one specimen, in order to ascertain the presence or absence of starch. No starch was found, but the iodine brought out a very remarkable structure on the surface of the organism, which certainly must be held to indicate the existence of a cuticular pellicle. The structure in question consisted of exceedingly fine granules (fig. 7), which, when a portion of the margin of the body was focussed, so as to give an optical section, had the appearance represented in fig. 6. The regular disc-like form of Lithamœba and the peculiar character of its hernia-like pseudopodia are quite in accordance with the existence of a cuticular pellicle, which must be inferred from the punctate structure rendered evident by iodine. The cuticle of *Lithamœba* is not a highly-developed one, like those of *Amphizonella*, or of *Amphitrema*, which leave portions of the body unprotected, whence the naked protoplasm can be extruded, but it is of a delicate and easily ruptured consistency, bursting, as it were, sometimes at one point, sometimes at another, in order to allow the contained protoplasm nakedly to expose itself in a hernia-like excrescence.

Pseudopodia.—The hernia-like pseudopodia of the same specimen as that drawn in fig. 1 are seen in fig. 2, the organism being represented in a state of activity. The extrusion of these masses seems to begin with a minute rupture of the cuticle. Through the orifice thus produced the fluid protoplasm exudes in a spherical form, and as it increases in quantity the rupture of the cuticle is increased, whilst concretions from the more central portion of the disc-like body flow into the enlarging lobe. With great rapidity the whole extrusion now appears to fuse once more with the disc, and a new rupture and extrusion takes place at another point of the margin. A new cuticular pellicle must be formed very rapidly on the surface of the hernia-like extrusions of protoplasm.

I did not observe in *Lithamœba* any filamentous or elongated pseudopodia, such as are known to accompany hernia-like pseudopodia in *Pelomyxa*.

Contractions of the vacuole.—During the movements of the specimen (fig. 1, fig. 2) the large central vacuole was seen to burst and discharge a *portion* of its contents to the exterior but it did not entirely collapse. Its walls fell together in such a way as to produce two smaller vacuoles,

together of less capacity than the first vacuole. These slowly increased in size, and after a time fused together to form one large vacuole, precisely like that from which they were derived.

Lithamœba discus is thus seen to be a uninucleate form with contractile vacuole. In the vacuolar differentiation of its protoplasm, its concretions, and hernia-like pseudopodia, it presents affinity with the multinucleate Pelomyxa, which has crystalline bodies in place of concretions, and no contractile vacuole.

In the structure of its nucleus and delicate cuticle *Lithamœba* is unlike any other form, whilst the combination of characters which it presents entitles it to a very distinct position amongst the Amœboid Gymnomyxa.

The concretions appear to be, very probably, only a larger form of the refringent granules which are present in great quantity in the protoplasm of the common large Amœbæ.

On the Structure *of the* Vertebrate Spermatozoon.

By Heneage Gibbes, M.B. (With Plate XXIV.)

In making an examination into the structure of the spermatozoa of Vertebrate animals those of the Amphibia, such as the *Triton cristatus* and *Salamandra maculata*, from their large size, afford the best examples. Taking then the living spermatozoon of either of these animals in the fresh condition just removed from the body we find the following appearances, shown in figs, 1 and 2, of *Salamandra maculata*, and fig. 3, of *Triton cristatus*.

Fig. I was drawn from a specimen of *Salamandra maculata*, mounted in a ½ per cent. solution of sodium chlorate.

Fig. 2, also in the same solution, under a lower power.

Fig. 3, spermatozoon of *Triton cristatus*, had been placed in a solution of chromate of ammonium and then mounted in glycerin.

From these illustrations it will be seen that the spermatozoon consists of (*a*) a *long-pointed head*, at the base of which is (*b*) an *elliptical structure* joining the head to (*c*) a long filiform *body*; (*d*) a fine *filament*, much longer than the body, is connected with this latter by (*e*) a homogeneous *membrane*.

The head as it appears in the fresh specimen has a different refractive power to the rest of the organism, and with a high power appears to be a light green colour; there is also a central line running up it, from which it appears to be hollow.

The elliptical structure at the base of the head connects it with the long thread-like body, and the filament seems to spring from it.

Whilst the spermatozoon is living this filament is in constant motion; at first this is so quick that it is difficult to see it, but as its vitality becomes impaired the motion gets slower, and it is then easily perceived to be a continuous waving from side to side.

When the connecting membrane is thrown into folds as the motion gets slower it is readily seen with a high power, but it is only visible in the fresh specimen, and disappears entirely on the application of glycerin.

This moving filament forms a most beautiful object under a moderately high power; it can be seen with Crouch's $\frac{1}{5}$ or Zeiss' D, but with Powell and Lealand's $\frac{1}{8}$ immersion on the new formula, it is seen to perfection.

The constant wavy motion gives one the idea that a fine thread is being constantly poured out from the base of the head, and it is difficult at first to realise what the motion is.

After a large number of experiments with reagents, I found that after placing the spermatozoon in a 5 per cent. solution of chromate of ammonium the body and filament can be stained with one reagent, while the head would take another. This is best shown by staining the spermatozoon first deeply with hæmatoxylin, when it will be found that the body and filament show the colour well, but the head scarcely at all, and staining it then in a weak solution of aniline blue; if it be not left in this fluid too long the head will be found a bright blue, while the body and filament remain coloured with the hæmatoxylin.

I have always found THAT THE ELLIPTICAL STRUCTURE uniting the head and body REMAINED OF THE SAME COLOUR AS THE BODY AND FILAMENT. It is a difficult thing to do this double staining well, since a slight mistake in the time of immersion or in the strength of the solution alters the result of the whole experiment, and although I have had numberless failures, I have succeeded in so many instances that I am confident *the substance of which the head is composed shows a different chemical reaction to the rest of the organism.*

With regard to the existence of a homogeneous membrane

connecting the filament to the body, this membrane at first seemed doubtful, and the filament appeared to be unconnected with the body; but with a high power the membrane can be recognised in the fresh state, and it will invariably he found that when the spermatozoon is curved, as it frequently is, and often lying in a double curve, the filament will always be found placed at a certain distance from the convexity of each curve; this distance varies a little in individual cases.

If, while examining a specimen in salt solution or distilled water, gentle pressure with the point of a needle be applied to the cover-glass so as to cause a slight vibration in the fluid, the filament will be seen to move to and fro but can never be forced further from the body than its natural distance, unless it has in any way been subjected to sufficient force to rupture the membrane, in which case it may be seen lying quite away from the organism to which it belongs. This seldom happens, and never when the experiment is carefully done. This would not be the case if the filament were free.

In the spermatozoa of *Triton cristatus* and also *Salamandra maculata*, prepared with a 5 part. solution of chromate of ammonium, and stained in picro-carmine, this membrane is not easily seen, and the filament appears as if free of the body, and twisted more or less like a spiral round the latter.

This appearance was originally described by Dr. Klein in this Journal, and its more minute examination was the primary object of my inquiry, which I carried on under his direction. Leydig ('Lehrbuch der Histologie') describes and figures (p. 493) the spermatozoon of Salamandrinæ as if possessed of a narrow undulating membrane attached to its body.

I next proceeded to examine some of the Mammalian spermatozoa to see if they possessed the filament just described, and in every instance I have found it. I have examined spermatozoa of horse, dog, bull, cat, rabbit, and guinea-pig, and in every case the above filament was found to exist.

The structure of the spermatozoon, as is well known, is in these instances slightly different from that of the spermatozoon of Amphibian animals. The long-pointed head is wanting, and the long filament does not seem to extend so far as in the Amphibia, but the Mammalian spermatozoon being so very much smaller it is very difficult to make out the filament in its whole extent. I have seen it best in the

spermatozoon of the horse, as shown in Fig. 4, and of that of the guinea-pig, Fig. 5.

In these spermatozoa there is an intermediate part between the head and tail, and on it the filament is seen plainly, but beyond this it is very indistinct.

In Reptilia I have only as yet examined the spermatozoon of the green lizard and slow worm, and in both of these I have found the filament, but very indistinct, and requiring a high magnifying power.

The speramatozoon of *Lacerta viridis* in the fresh state has a very peculiar appearance. The part corresponding to the elliptical body in the Amphibia is enveloped in a gelatinous mass somewhat resembling a leucocyte; it keeps in constant motion for a long time, and it is almost impossible to see any other part of it until it loses its vitality; the gelatinous mass keeps changing its shape as it moves with a quick jerky motion.

After a number of experiments in staining the spermatozoa of Mammals with several dyes, I found it almost impossible to obtain any such definite results as in the case of the larger spermatozoa of the Amphibia, and it occurred to me to try to attain the same result, viz. to show differences in chemical constitution of the different parts of the spermatozoon, by observing the effect produced by different acids and alkalies of varying strengths.

I obtained the most striking result with a solution of *chloride of sodium*, varying from ½ to 5 per cent; with this reagent I found that the head gradually dissolved away, together with the membrane connecting the filament to the body.

In Figs. 6, 7, 8, and 9 the effect of the chloride of sodium is shown

Taking a solution of ½ per cent. strength at the end of twenty-four hours, the head will be found in different stages of disintegration; some heads are not affected in the least, others are partially dissolved, while still others have become so faint as scarcely to be discerned. After another twenty-four hours, quite one half of the head will have altogether disappeared, but at the same time some heads will remain almost untouched.

The same result may be arrived at in a much shorter time by using a stronger solution.

It will be seen, by referring to Figs. 7 and 8, that the elliptical structure, the long filament, and the body, remain intact.

In the spermatozoon of *L. viridis*, the gelatinous mass

enveloping the head becomes also dissolved. In the guinea-pig the large flat head disappears, and that part only remains which is seen as a dark band when the head is *en profile*, as in c and d in Fig. 5.

The action of *Sodæ Bicarb.* is somewhat different; in about forty-eight hours the head becomes transformed into a mass of minute globules, as shown in Fig. 10, and after a time these disappear.

From the foregoing experiments I am justified in concluding—

1st. That the head of the spermatozoon is enclosed in a sheath, which is a continuation of the membrane which surrounds the filament, and connects it to the body, acting, in fact, the part of a mesentery.

2ndly. That the substance of the head is quite distinct in its composition from the elliptical structure, the filament, and the long body, and that it is readily acted upon by alkalies; these reagents have no effect, however, on the other part excepting the membranous sheath.

3rdly. That this elliptical structure has its analogue in the Mammalian spermatozoon; in the one case the head is drawn out as a long pointed process, in the other it is of a globular form and surrounds the elliptical structure.

4thly. That the motive power lies, in a great measure, in the filament and the membrane attaching it to the body.

In my next paper I propose to enter into the structure of the human spermatozoon and that of some of the invertebrata.

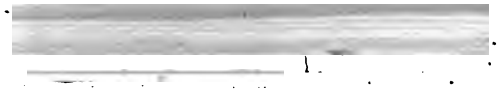
NOTES AND MEMORANDA.

New Record of Zoological Literature.—We would call the attention of naturalists to the following notice. "The Zoological Station at Naples has undertaken the publication of a new 'Zoological Record,' in which equal attention will be paid to all departments of zoology. A large staff of zoologists of various nationalities will act as recorders under the editorship of Professor J. V. Carus, of Leipzig; and the first volume, dealing with the literature of the current year, will appear in 1880. All those engaged in zoological work on any group of the animal kingdom, are invited to send copies of their papers to Professor J. V. Carus, Leipzig, Querstrasse 30, and to write on the address "For the *Jahresbericht*." Papers so sent will be distributed by Professor Carus amongst the recorders, and after being abstracted for the 'Record,' will be deposited in the Library of the Zoological Station at Naples.—ANTON DOHRN."

Mr. Bolton's Agency for the Supply of Microscopic Organisms.—Mr. Bolton, of 17, Ann Street, Birmingham, has supplied to me once a week by post, during the past year, a tube containing in a living state new or interesting forms of Protozoa, Entomostraca, Rotifera, &c. Every naturalist within a day's post of Birmingham should subscribe a guinea to Mr. Bolton's agency, and ensure the weekly receipt of one of his most interesting tubes. Mr. Bolton has sent out during the past year most of the more important forms of Rotifera, such as *Hydatina senta*, *Lacinularia socialis*, *Conochilus volvox*, *Melicerta* and *Œcistes*, *Stephanoceras* and *Floscularia*, &c. One form sent by him, viz. the *Rhinops vitrea*, of Dr. Hudson, is especially worthy of mention. Large Amœbæ and the commoner Ciliate Infusoria have been supplied by Mr. Bolton in abundance. Amongst rarer Ciliata supplied by him we may mention *Trachelius ovum* and *Zoothamnium arbuscula*. The work which Mr. Bolton is doing is not, however, limited to the distribution of forms already known; he has made some important addi-

tions to the British Fauna, for which he deserves the warmest support and encouragement of zoologists. About three months ago I received from him a tube containing specimens of an Entomostracon which he was unable to identify, rightly considering it new to this country. The form proved to be the beautiful *Leptodora hyalina* of Lilljeborg. A few days later another tube was sent by him, containing a species which I identified as the *Hyalodaphnia Kahlbergensis* of Schödler. These two very fine Entomostraca were obtained by Mr. Bolton from a deep reservoir at Olton. Besides these I have to thank Mr. Bolton for the new Protozoon *Lithamœba discus*, described in the present number of the Journal. Last autumn, from the same source, I received an abundant supply of one of those very interesting spiculate Heliozoa, which my colleague, Mr. Archer, of Dublin, was the first to make known to zoologists. The specimens forwarded by Mr. Bolton proved to be the *Raphidiophrys pallida*, a species named by Prof. F. Eilhard Schulze, and assigned by him to Archer's genus.

Mr. Bolton has also during the year supplied me with the finest specimens of *Hydra fusca* which I have seen, with *Volvox*, *Uroglena*, and other similar forms. A few marine organisms have been distributed by him, namely, the interesting disc-like larvæ of the Polyzoon *Alcyonidium*, and the delicate polyp *Lucernaria auricula*.—E. Ray Lankester.



EXPLANATION OF PLATE II.

SERIES D.—Sections chosen at intervals from a complete series traversing the peritoneal opening of the Müllerian duct, the remnant of the head-kidney, and the termination of the Müllerian duct. Zeiss, C, ocul. 3 (reduced one-third).

Nos. 1 and 2.—Sections through the persistent anterior opening of the head-kidney (abdominal opening of Müllerian duct). The approach of the Wolffian duct to the groove may be seen by a comparison of these two figures. In the sections in front of these (not figured) the two are much more widely separated than in No. 1.

No. 3.—Section through the Müllerian duct, just posterior to the persistent opening.

Nos. 4 and 5.—Remains of the ridges, which at an earlier stage connected the first and second grooves, are seen passing from the Müllerian duct to the peritoneal epithelium.

No. 6.—Rudiment of the second groove (gr_2.) of the head-kidney.

Between 6 and 7 is a considerable interval.

No. 7.—All traces of this groove (gr_2.) have vanished, and the Müllerian duct is quite disconnected from the epithelium.

No. 8.—Rudiment of the third groove (gr_3.).

No. 9.—Müllerian duct quite free in the space between the peritoneal epithelium and the Wolffian duct, in which condition it extends until near its termination.

Between Nos. 9 and 10 is an interval of eight sections.

No. 10.—The penultimate section, in which the Müllerian duct is seen. A lumen cannot be clearly made out.

No. 11.—The last section in which any trace of the Müllerian duct is visible. No line of demarcation can be seen separating the solid end of the Müllerian duct from the ventral wall of the Wolffian duct.

FIGS. E. and F.—Sections through the glomerulus of the head-kidney from an embryo prior to the appearance of the head kidney. Zeiss, B, ocul. 2. A comparison of the two figures shows the variation in the thickness of the stalk of the glomerulus. E.—Section anterior to the foremost Malpighian body. F.—Section through both the glomerulus of the head-kidney and that of a Malpighian body. The two are seen to be connected.

SERIES H.—Consecutive sections through the hind end of the Müllerian duct, from an embryo in which the head-kidney was only represented by a rudiment. (The embryo was, perhaps, very slightly older than that from which Series D was taken.) Zeiss, C, ocul. 3 (reduced one third).

No. 1.—Müllerian duct is without a lumen, and quite distinct from the Wolffian wall.

No. 2.—The solid end of the Müllerian duct is no longer distinct from the internal wall of the Wolffian duct.

No. 3.—All trace of the Müllerian duct has vanished.

SERIES I.—Sections through the hinder end of the Müllerian duct from an embryo of about the middle of the sixth day. Zeiss, C, ocul. 2 (reduced one third).

No. 1.—The Müllerian duct is distinct and small.

No. 2.—Is posterior by twelve sections to No. 1. The Müllerian duct is dilated, and its cells are vacuolated.

No. 3.—Penultimate section, in which the Müllerian duct is visible; it is separated by three sections from No. 2.

No. 4.—Last section in which any trace of the Müllerian duct is visible; the lumen, which was visible in the previous section, is now absent.

No. 5.—No trace of Müllerian duct. Nos. 3, 4, and 5, are consecutive sections.

FIG. K.—Section through the hind end of the abdominal opening of the Müllerian duct of a chick of 123 hours. Zeiss, C, ocul. 2 (reduced one-third). It illustrates the peculiar cord connecting the Müllerian and Wolffian ducts.

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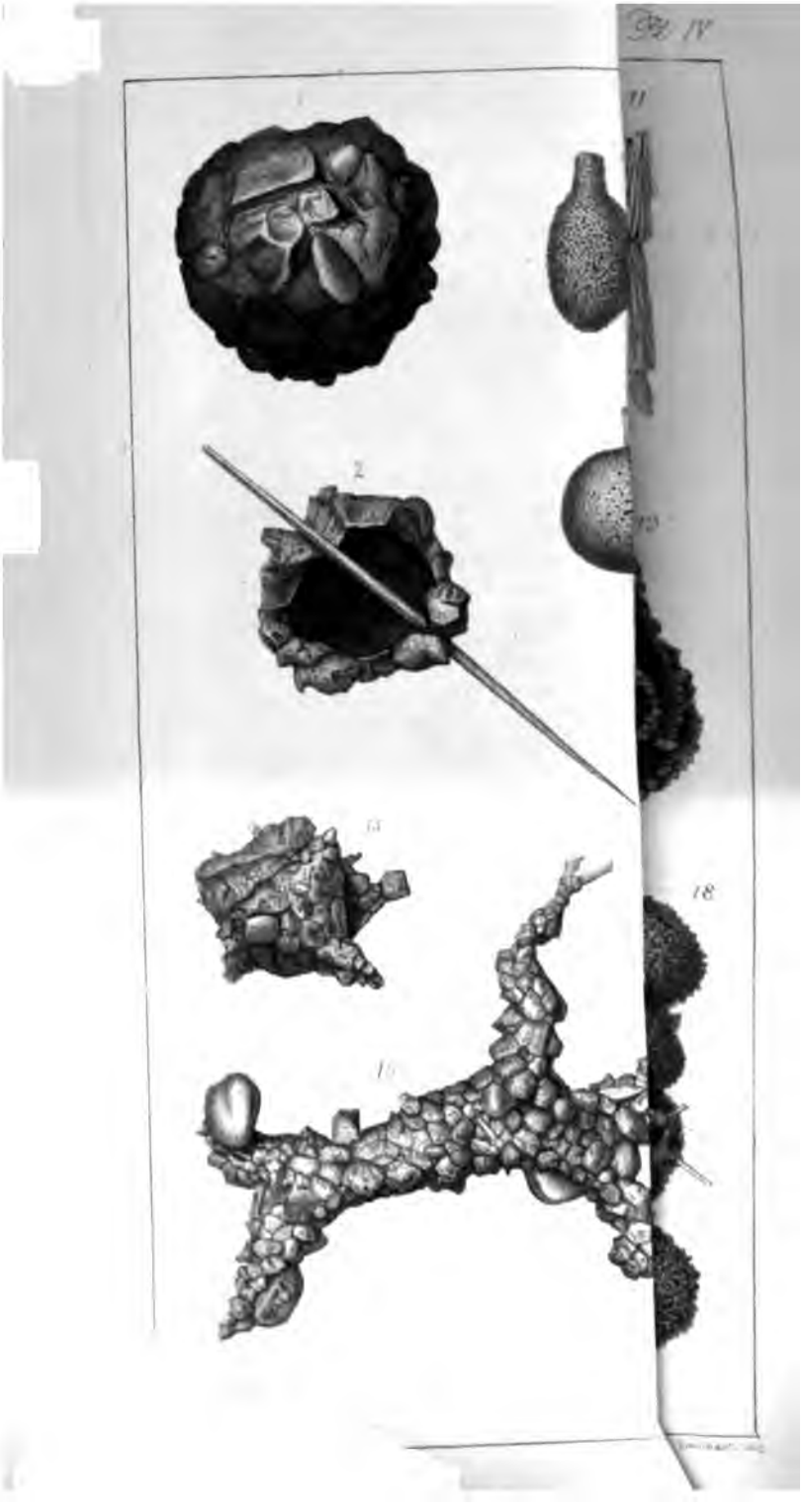
Pl. IV
11
2
13
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17

EXPLANATION OF PLATES III, IV, & V,

Illustrating Mr. Henry B. Brady's "Notes on some of the Reticularian Rhizopoda of the 'Challenger' Expedition."

PLATE III.

FIGS. 1, 2.—*Pelosina variabilis*, n. sp. Magnified 9 diameters.

FIG. 3.—Section of the same showing the thickness and texture of the test. × 9 diam.

FIG. 4.—*Pelosina rotundata*, n. sp. × 20 diam.

FIG. 5.—Transverse section of the same showing the interior and the thickness and texture of the test. × 15 diam.

FIGS. 6, 7.—*Aschemonella scabra*, nov. × 14 diam.

FIG. 8.—*Marsipella granulosa*, n. sp. × 12 diam.

FIG. 9.—Specimen of the same species laid open longitudinally to show the interior and the texture of the test. × 15 diam.

FIG. 10.—*Rhabdammina linearis*, n. sp. × 20 diam.

FIG. 11.—The same laid open longitudinally. × 20 diam.

FIG 12.—*Jaculella acuta*, nov. × 9 diam.

FIG. 13.—The same laid open; specimen slightly broken at the ends in grinding. × 9 diam.

FIGS. 14, 15.—*Hyperammina ramosa*, n. sp. × 16 diam.

PLATE IV.

FIG. 1.—*Psammosphæra fusca*, F. E. Schulze. Magnified 40 diameters.

FIG. 2.—The same; specimen built on a sponge spicule, laid open so as to show the interior. × 50 diam.

FIG. 3.—*Reophax difflugiformis*, n. sp. × 50 diam.

FIG. 4.—*Hormosina globulifera*, n. sp. Specimen arrested in growth after the formation of a single large chamber. × 20 diam.

FIG. 5.—The same; with two chambers. Large specimens with four or five segments are not uncommon. × 20 diam.

FIG. 6.—*Hormosina ovicula*, n. sp. × 12 diam.

FIG. 7.—*Reophax nodulosa*, n. sp. × 12 diam.

FIG. 8.—The same laid open to show the interior structure. × 12 diam.

FIG. 9.—*Reophax membranacea*, n. sp. × 40 diam.

FIGS. 10, 11.—*Reophax spiculifera*, n. sp. × 40 diam.

FIGS. 12, 13.—*Astrorhiza catenata*, Norman. × 25 diam.

FIG. 14.—*Astrorhiza cornuta*, n. sp. × 20 diam.

FIG. 15.—The same. × 15 diam.

FIG. 16.—*Rhizammina algæformis*, nov. Natural size.

3
a
9
b
8
15
16

2.
a
b
c
d
e
3.
10.
11.
9.
15. a
2. c
24.
b
e
d
f

DESCRIPTION OF PLATE VI,

trating Professor Bütschli's "Researches on Flagellate Infusoria and Allied Organisms."

ughout the figures, *n* indicates nucleus, *v* contractile vacuole, and hagus.

1.—*Spumella termo* (Ehrb.), Clark.
a to c, an individual in different stages of the ingestion of food.

2.—*Spumella termo*, in five successive stages of transverse division.

3.—*Spumella truncata*, Fresenius.

4.—*Chromulina ochracea*, Ehrb.
a, b, two individuals seen from the flat side, the flagellum not plainly observed and therefore not drawn.
c, an individual seen from the narrow side.

5.—Flagellate-like organism from the alimentary canal of a free-nematoid (*Trilobus pellucidus*, Bast.).
a, a large number of individuals sticking together by their hinder ends.
b, a single individual.

6.—*Anthophysa vegetans*, O. F. Müller.
a, terminal branch of the stem with a colony.
b, an individual in the act of division.

7.—*Codosiga botrytis* (Ehrb.), Fresenius.
a, a colony.
b, a single individual.
c, a single individual with its collar expanded.
d, the same with its collar contracted.
e, an individual externally beset with Bacteria.

8.—*Salpingœca gracilis*, Clark (?).

9.—*Salpingœca amphoridium*, Clark (?).

10.—*Salpingœca Clarkii*, n. sp.

11.—Salpingœca-like organism (see p. 75).

12.—*Bicosœca lacustris*, Clark (?).
a, a colony.
b, two cups, of which only the upper contains an animal, and that in a retracted state.
c, an individual.
d, the same turned half round.

13.—*Dinobryon sertularia*, Ehrb.
a, a colony.
b, a cup containing two animals resulting from division, of which the anterior will immediately secrete a new cup.
c, a cyst.

DESCRIPTION OF PLATE VI—*Continued.*

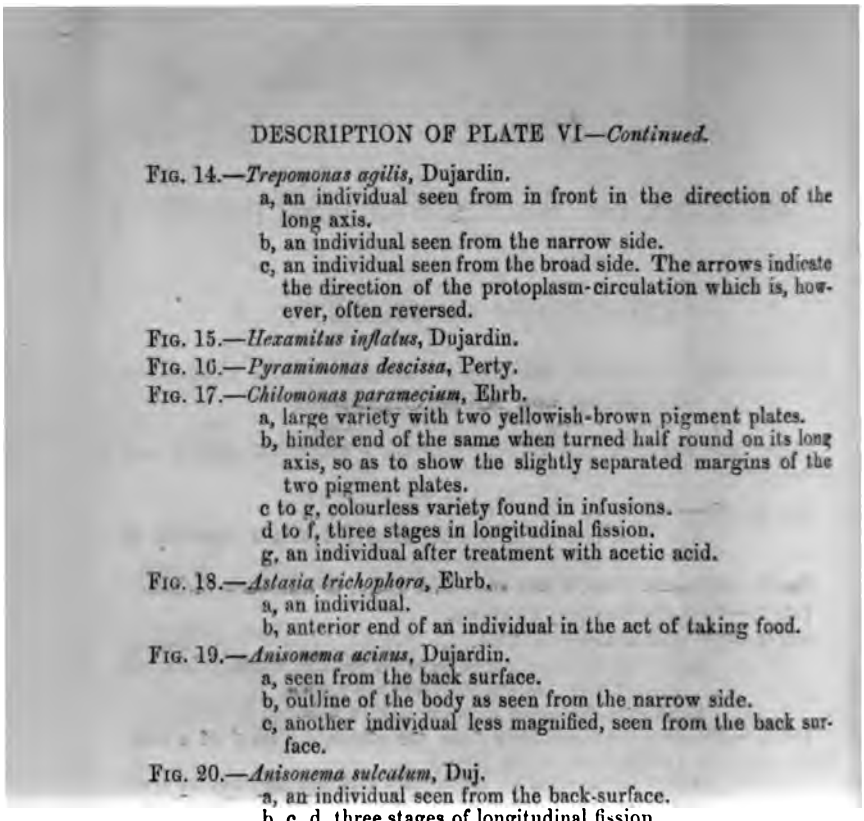


FIG. 14.—*Trepomonas agilis*, Dujardin.
a, an individual seen from in front in the direction of the long axis.
b, an individual seen from the narrow side.
c, an individual seen from the broad side. The arrows indicate the direction of the protoplasm-circulation which is, however, often reversed.

FIG. 15.—*Hexamitus inflatus*, Dujardin.

FIG. 16.—*Pyramimonas descissa*, Perty.

FIG. 17.—*Chilomonas paramecium*, Ehrb.
a, large variety with two yellowish-brown pigment plates.
b, hinder end of the same when turned half round on its long axis, so as to show the slightly separated margins of the two pigment plates.
c to g, colourless variety found in infusions.
d to f, three stages in longitudinal fission.
g, an individual after treatment with acetic acid.

FIG. 18.—*Astasia trichophora*, Ehrb.
a, an individual.
b, anterior end of an individual in the act of taking food.

FIG. 19.—*Anisonema acinus*, Dujardin.
a, seen from the back surface.
b, outline of the body as seen from the narrow side.
c, another individual less magnified, seen from the back surface.

FIG. 20.—*Anisonema sulcatum*, Duj.
a, an individual seen from the back-surface.
b, c, d, three stages of longitudinal fission.
e, f, two stages of fission only drawn in outline to show the nucleus as seen in an acetic acid preparation.

FIG. 21.—*Lophomonas*, Stein.
a, b, *Lophomonas Blattarum*, Stein.
c, d, *Lophomonas striata*, Bütschli.

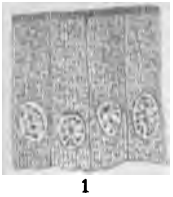
FIG. 22.—*Uvella virescens*, Ehrb.
a, a small colony; *x*, a Chlorogonium-like frequent parasite of these colonies.
b, c, individuals coloured by carmine so as to show the nucleus distinctly.
d, an individual in the act of fission.

FIG. 23.—*Uroglena volvox*, Ehrb. A group of five individuals taken from a colony, amongst them a large one.

FIG 24.—Unknown flagellate (see p. 99).
a, flagellate phase.
b, nuclearia-like Rhizopodous phase.

FIG. 25.—Flagellum-bearing peculiar rhizopod-like organism (see p. 100).
a, creeping phase.
b, swimming phase.

FIG. 26.—*Amœba Blattæ*, n. sp.
a, a medium-sized, uninuclear, very clearly fibrillated specimen.
b, nucleus of a large uninuclear specimen; *h*, case of the nucleus.
c, portion of a similar nucleus with a peculiar prolongation.
d, multinuclear cyst belonging to this species.



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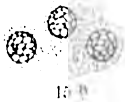


15 B

16.

17.

20.

EXPLANATION OF PLATE VII,

Illustrating Dr. Klein's "Observations on the Structure of Cells and Nuclei."

FIG. 1.—Epithelium covering the surface of a villus, from a section through small intestine of pig.

FIG. 2.—Epithelium lining a Lieberkühn's crypt of large intestine of pig.

FIG. 3.—Goblet cells of a Lieberkühn's crypt of large intestine of pig; *a*, as viewed from the surface; *b*, as viewed from the side.

FIG. 4.—Epithelium lining the tube of a mucous gland of tongue of dog.

FIG. 5.—Part of a tube of mucous gland of epiglottis of a child; at *a*, the epithelial cells are in state of secretion; at *b*, in a state of rest.

FIG. 6.—Epithelium lining a tube of Brunner's gland of duodenum of dog. The epithelial cells after prolonged secretion.

FIG. 7.—Epithelium of Brunner's gland of dog in a state of secretion.

FIG. 8.—The same epithelium viewed from the surface.

FIG. 9.—Part of a tube of the epididymis of full-grown dog. *a*, ciliated epithelium; in the depth is seen a row of deeply-stained nuclei belonging to a layer of small cells; *b*, muscular coat.

FIG. 10.—Two epithelial cells of the same organ more highly magnified.

FIG. 11.—Part of a longitudinal section of the tube of a sweat-gland of ear-lobe of pig. *a*, epithelial lining; *b*, muscular coat; *c*, membrana propria.

FIG. 12.—Section through the tube of a mucous gland of pharynx of dog; *c*, mucous cells lining the lumen; *p*, parietal cells. The details of structure of the individual cells in this and the next fig. (13) are not carried out; they are identical with those shown in fig. 17.

FIG. 13.—From a section through submaxillary gland of dog. *c*, mucous cells; *p*, parietal cells.

FIG. 14 A.—Interstitial epithelial cells—so-called plasma-cells—of testis of full-grown cat.

FIG. 14 B.—Same elements of testis of guinea-pig.

FIG. 15 A.—Epithelial cells lining a seminal tube of testis of cat.

FIG. 15 B.—Same elements of testis of guinea-pig.

FIG. 16.—Part of sebaceous gland of skin of sheep. *a*, peripheral epithelial cells; *b*, central ones.

FIG. 17.—Part of the tube of a peptic gland of dog. The tube is cut slightly obliquely. *c*, chief cells; *p*, parietal cells.

FIG. 18 A.—Epithelial cells of the middle layers of epithelium lining the œsophagus of a child. The connection of the network of contiguous cells should be more distinct.

FIG. 18 B.—Same elements more highly magnified, but only the nuclei are represented in detail.

FIG. 19.—Epithelial cells of the rete Malpighii of skin of sheep.

FIG. 20.—Liver cells of guinea-pig.

FIGS. 1, 3, and 10 drawn with Hartnack's Ocul. II, Obj. Immersion 10. FIGS. 14 A and 18 B, Hartnack III, 10 Im. The other figures are drawn with Hartnack's Ocul. II, Zeiss' Obj. F.

EXPLANATION OF PLATES IX, X, XI,

Illustrating Nikolas Kleinenberg's paper on the Development of the Earth-worm, *Lumbricus trapezoides*, Dugès.

The references are the same in all the figures.

as. Aperture of the segmentation cavity. *cb.* Buccal cavity. *cc.* General body cavity or cavity of the zoonites. *cd.* Digestive cavity. *cm.* The large primitive cells of the mesoderm (mesoblasts). *com.* Commissure of the œsophageal collar. *cs.* Segmentation cavity. *cw.* Cord uniting the twin embryos, or its single cells. *ec.* Ectoderm. *en.* Endoderm. *eo.* Ectodermic epithelium of the mouth and of the œsophagus. *gc.* Cephalic ganglion. *lso.* Somatic lamina. *lsp.* Splanchnic lamina. *m.* Muscle plate. *mes.* Mesoderm. *n.* Ventral nerve-cord. *pc.* Cephalic germinal streak. *pp.* Primitive ventral germinal streak. *sn.* Ventral furrow.

PLATE IX.

FIG. 1.—Segmented egg, seen from above.

FIG. 2.—Germinal bladder formed of a single layer of cells. The segmentation cavity opens externally. Figs. 1 and 2, Zeiss' objective DD, ocular 3.

FIG. 3.—Solid germinal sphere, in which the rudiments of the layers for the first embryo are visible.

FIG. 4.—A rather later stage, in which the formation of the second embryo has begun. Longitudinal section.

FIG. 5.—Longitudinal section of a more developed stage.

FIG. 6.—Twin-embryos. The one on the right hand is rather the more developed.

FIG. 7.—Embryos nearer the period of separation.

FIG. 8.—Longitudinal section of a double embryo, in profile.

FIG. 9.—Longitudinal horizontal section of the same.

FIG. 10.—Advanced embryo developing the second embryo in the form of a bud (X).

N.B. Figs. 2 to 10 represent optical sections.

FIG 11*a*.—Transverse section of the posterior end of a very young embryo.

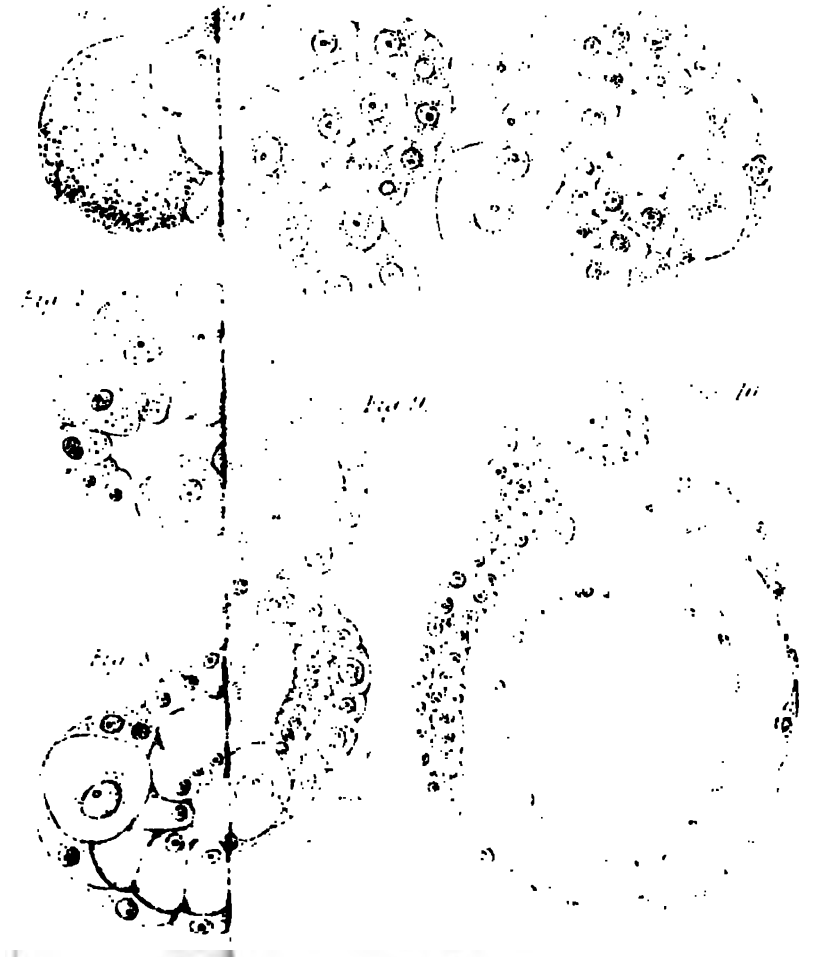
FIG. 11*b*.—From the same embryo more in front.

FIG. 12.—Transverse section of the posterior part of a more developed embryo.

FIG. 13.—Section through the middle of the body of a more advanced embryo. *f.* Fissure in the mesoderm.

Figs. 3 to 13. Zeiss' obj. F, ocul. 1.

FIG. 14.—The lower part of a section of the anterior extremity of a more developed embryo. Obj. DD, ocul. 3.



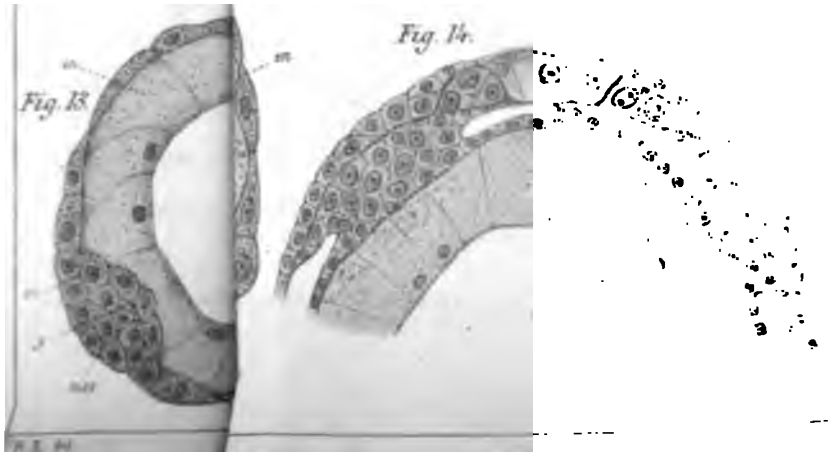
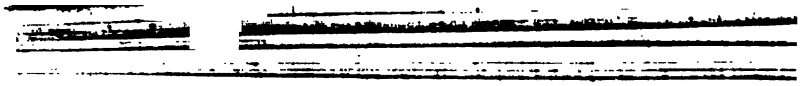
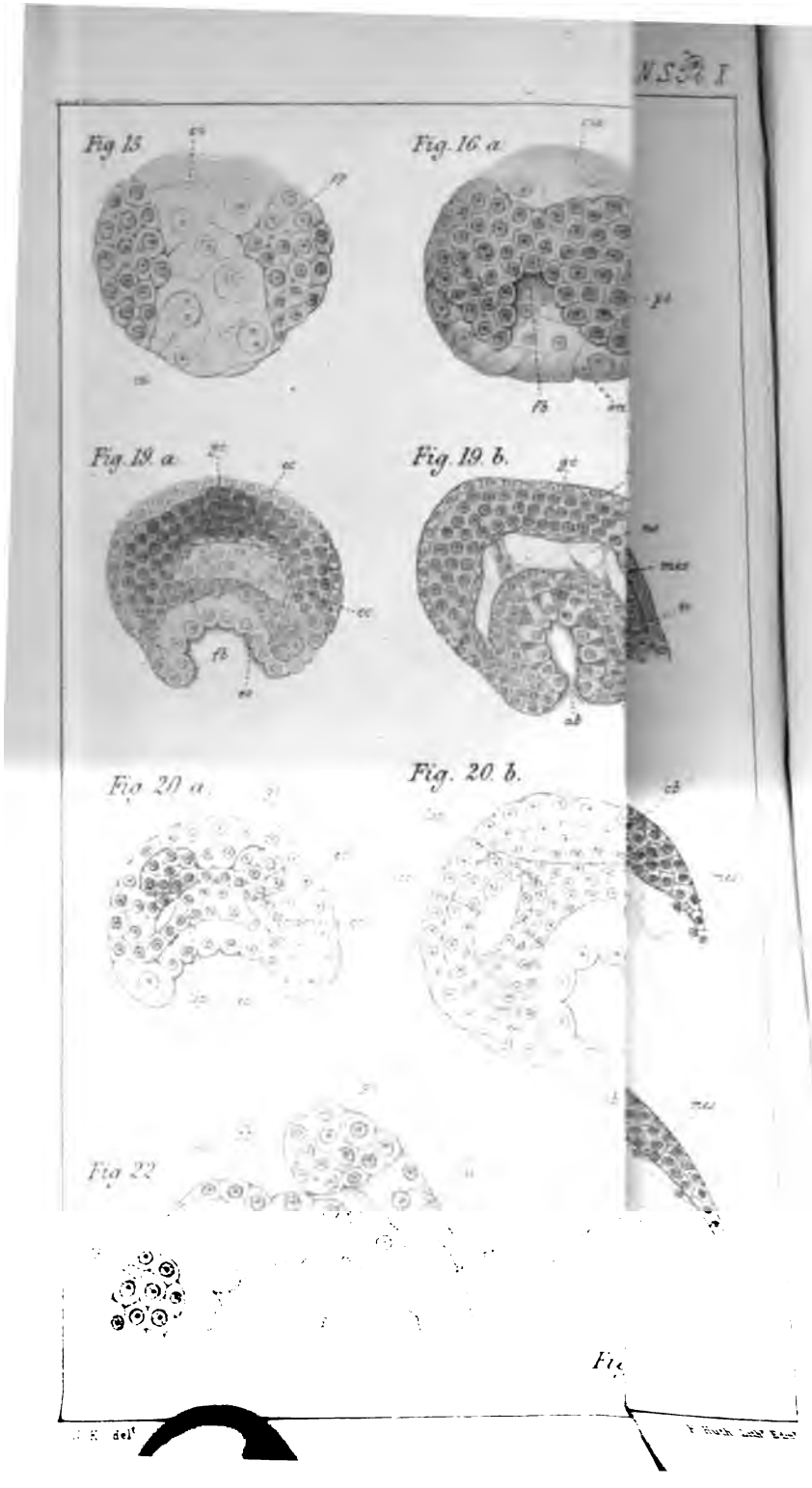


Fig. 13.
Fig. 14.




N.S. I
Fig 15
Fig. 16. a
Fig. 19. a.
Fig. 19. b.
Fig 20 a
Fig. 20. b.
Fig 22

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ANATION OF PLATES IX, X, XI—*continued.*

PLATE X.

sverse section of the head end of a very young embryo.

same of an embryo 0·2 mm. in length.

tion immediately behind 16*a*.

ion of the head end of a rather more developed embryo.

ion of the head end of an embryo 0·23 mm. in length.

15 to 18. Obj. DD, ocul. 3.

, *d*.—Successive sections of the head of an embryo 0·5 mm. Obj. DD, ocul. 1.

.—Succesive sections of the head of an embryo 0·4 mm. in Obj. DD, ocul. 3.

.—Longitudinal horizontal sections of the head end of an ·6 mm. in length, going from the ventral to the dorsal face. fth, *b* the sixth, *c* the ninth, and *e* the tenth of the series. ocul. 1.

gitudinal vertical (sagittal) section through the middle of the art of an embryo 0·22 mm. in length. Obj. DD, ocul. 3.

erior portion of a *longitudinal vertical* (sagittal) section of o 0·6 mm. in length. Obj. DD, ocul. 3.

tical section in the median line of an embryo more than a in length. Obj. DD, ocul. 1.

PLATE XI.

.—Three successive sections through the posterior part of llary plate of an embryo 3·0 mm. in length, going from rwards.

.—Successive sections in the same direction, from the an- rt of the same embryo.

, *d*, *e*.—Successive sections in the same direction, from an f 4·5 mm. in length. All the figures in this plate were drawn DD, ocul. 3, Zeiss.

DESCRIPTION OF PLATE XII,

Illustrating Surgeon T. R. Lewis's paper on "The Nematoid Hæmatozoa of Man," Figs. 1—13. The mature *Filaria sanguinis-hominis*, ♂ and ♀, and some of the developmental stages of the Embryos.

FIG. 1.—Anterior portion of mature helminth. Magnified 100 diam.

FIG. 2.—Middle portion of parasite showing alimentary canal; and the uterine tubules filled with ova. × 100 diam.

FIG. 3.—Ova and embryos. × 300 diam.

FIG. 4.—A portion of the male worm, with alimentary and sperm tubules escaping at one of the torn ends. × 100 diam.

FIG. 5.—Embryo recently ingested by a mosquito. × 300 diam.

FIGS. 6, 7.—Early changes undergone by the embryos in the mosquito.

FIG. 8.—?

FIG. 9.—More advanced stage of the development of the embryo. × 300 diam.

FIG. 10.—The "sausage-form" stage of development of the embryos. × 300 diam.

FIG. 11.—The embryos acquire more worm-like proportions. × 100 diam.

FIG. 12.—A still further advanced stage: the alimentary canal distinguishable. × 100 diam.

FIG. 13.—Ditto: more highly magnified (300 diameters). The re-agent applied has caused the contents of the caudal end to contract.

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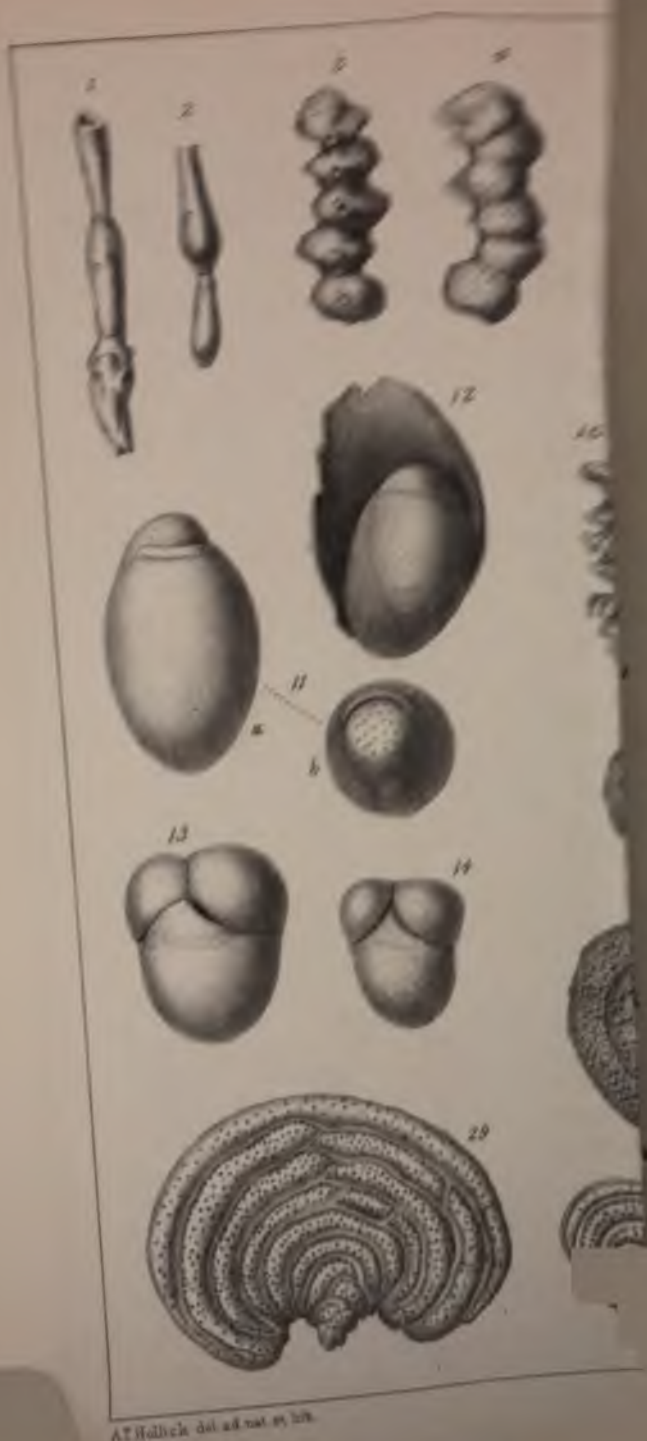


A.T. Hollick del. ad nat. et lith.

EXPLANATION OF PLATE VIII,

ıting Mr. Henry B. Brady's "Notes on some of the ılarian Rhizopoda of the 'Challenger' Expedition."

1, 2.—*Nubeculoria tibia*, J. and P. × 30 diameters.
3, 4.—*Dactylopora eruca*, P. and J. × 50 diam.
.—*Frondicularia spathulata*, nov. × 30 diam.
a, lateral aspect; *b*, end view.
.—*Frondicularia compta*, nov. × 50 diam.
.—*Flabellina cuneata* (von Münster). × 50 diam.
8, 9.—*Flabellina foliacea*, nov. × 50 diam.
0.— — — — × 35 diam.
1.—*Chilostomella ovoidea*, Reuss. × 40 diam.
a, lateral aspect; *b*, end view.
2.—Broken specimen, showing internal structure. × 40 diam.
13, 14.—*Allomorphina trigona*, Reuss. × 60 diam.
15, 16.—*Uvigerina porrecta*, nov. × 55 diam.
17, 18.—*Uvigerina interrupta*, nov. × 55 diam.
19—21.—*Sagrina virgula*, nov. × 55 diam.
22—24.—*Sagrina divaricata*, nov. × 55 diam.
5.—*Spirillina inæqualis*, nov. × 75 diam.
a, lateral; *b*, periphero-lateral aspect.
6.—*Spirillina limbata*, nov. × 60 diam.
a, lateral; *b*, periphero-lateral aspect.
7.—*Spirillina obconica*, nov. × 60 diam.
a, lateral; *b*, periphero-lateral aspect.
8.—*Spirillina tuberculata*, Brady. × 40 diam.
a and *b*, upper and lower surfaces.
29, 30.—*Pavonina flabelliformis*, d'Orb. × 50 diam.
1.—*Planorbulina echinata*, nov. × 60 diam.
32, 33.—*Ramulina globulifera*, nov. × 30 diam.

DESCRIPTION OF PLATES XIII, XIV.

Illustrating Dr. Milnes Marshall's Paper on the "Morphology of the Vertebrate Olfactory Organ."

Each figure has been drawn from a single section by the aid of a Hartnack camera. The numbers attached indicate, in diameters, the magnifying power employed in each case. The majority of the figures are of a semi-diagrammatical nature, the mesoblast being in nearly all cases omitted for the sake of clearness; the outlines are, however, strictly accurate in all cases. Figures 21, 22, 27, and 28 are drawn from sections kindly lent me for the purpose by Mr. Balfour; the rest are from specimens of my own preparation.

ALPHABETICAL LIST OF REFERENCES.

al. Alimentary canal. *al'.* Anterior prolongation of alimentary canal. *aor.* Dorsal aorta. *a. r.* Anterior root of a spinal nerve. *aud.* Auditory vesicle. *b. a.* Branchial artery. *br.* 1. First branchial arch. *br.* 2. Second branchial arch. *c. h.* cerebral hemisphere. *f. b.* forebrain. *g.* gill. *h.* 2. Second head-cavity. *h. b.* Hindbrain. *hy.* Hyoid arch. *inf.* Infundibulum. *l. c.* Lachrymal cleft. *m. b.* Midbrain. *Mn.* Mandibular arch. *m. p.* Muscle plate. *Mx.* Maxillary arch. *n.* Notochord. *o. c.* Optic cup or eye. *olf.* Olfactory pit. *ol. v.* Olfactory vesicle or lobe. *r. i.* Inferior rectus muscle. *r. s.* Superior rectus muscle. *Sch.* Schneiderian folds. *sp.* Spinal cord. *tr.* Trabeculæ cranii. *v. c.* Visceral cleft. I. Olfactory nerve. II. Optic nerve. III. Third or oculomotor nerve. V. Trigeminal nerve. V *a.* Ophthalmic branch of the trigeminal nerve, or ramus ophthalmicus profundus. V 3. Inferior maxillary branch of the trigeminal nerve. VII. Facial nerve. VII *a.* Ophthalmic branch of the facial nerve, or ramus ophthalmicus superficialis. VIII. Auditory nerve. IX. Glossopharyngeal nerve. X. Vagus or pneumogastric nerve.

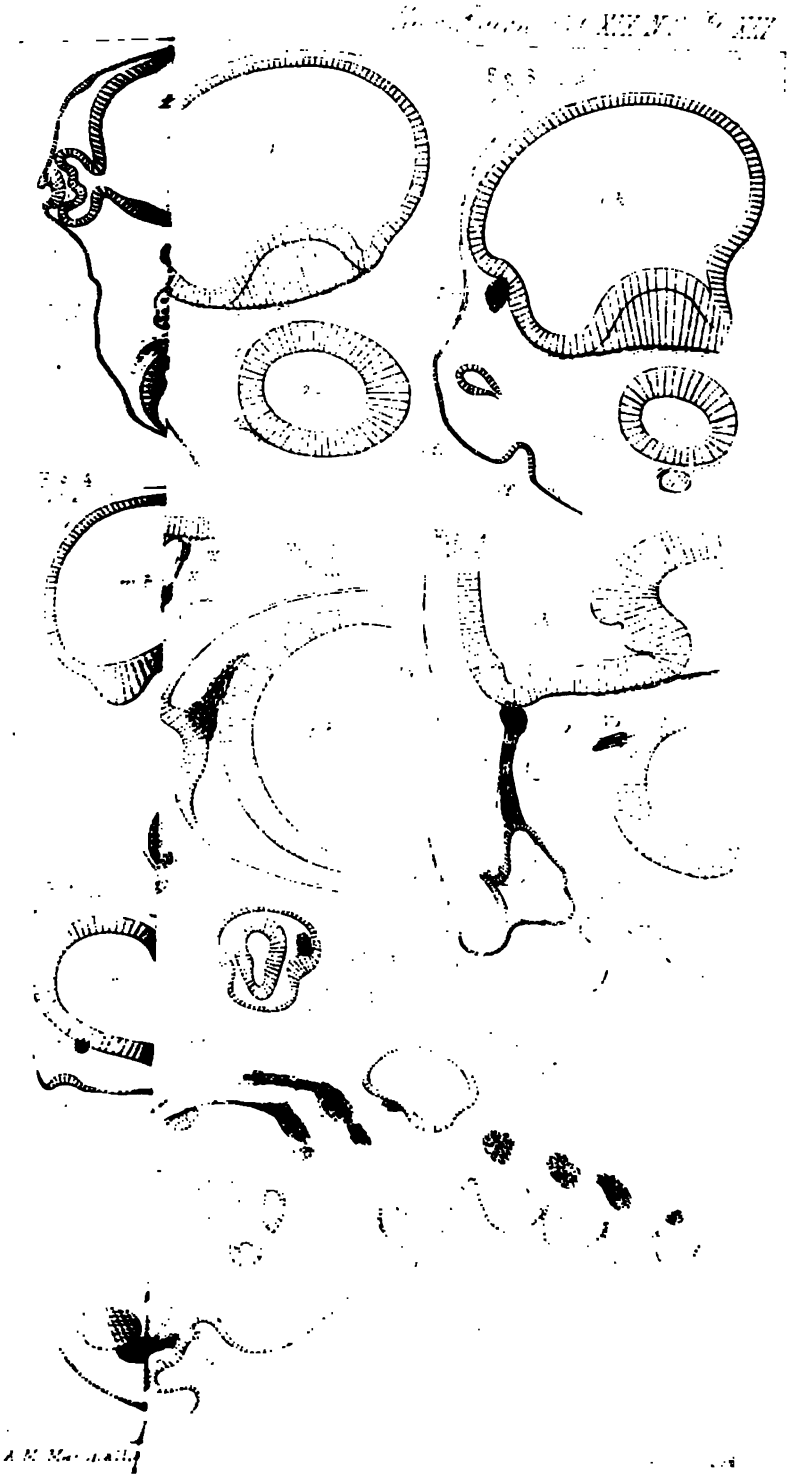
FIG. 1.—Longitudinal and horizontal section through the head of a fifty-four hours' chick embryo, showing early stage in the formation of the olfactory pits, also the visceral clefts with their communication with the exterior. Picric acid. × 35 diameters.

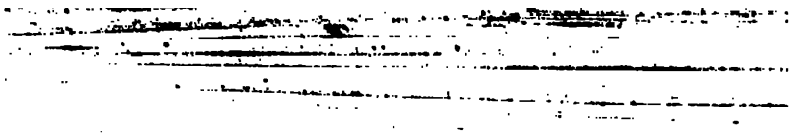
FIG. 2.—Longitudinal and vertical section through the fore part of the head of a sixty-four hours' chick embryo, showing olfactory nerve and pit. Picric acid. × 27 diam.

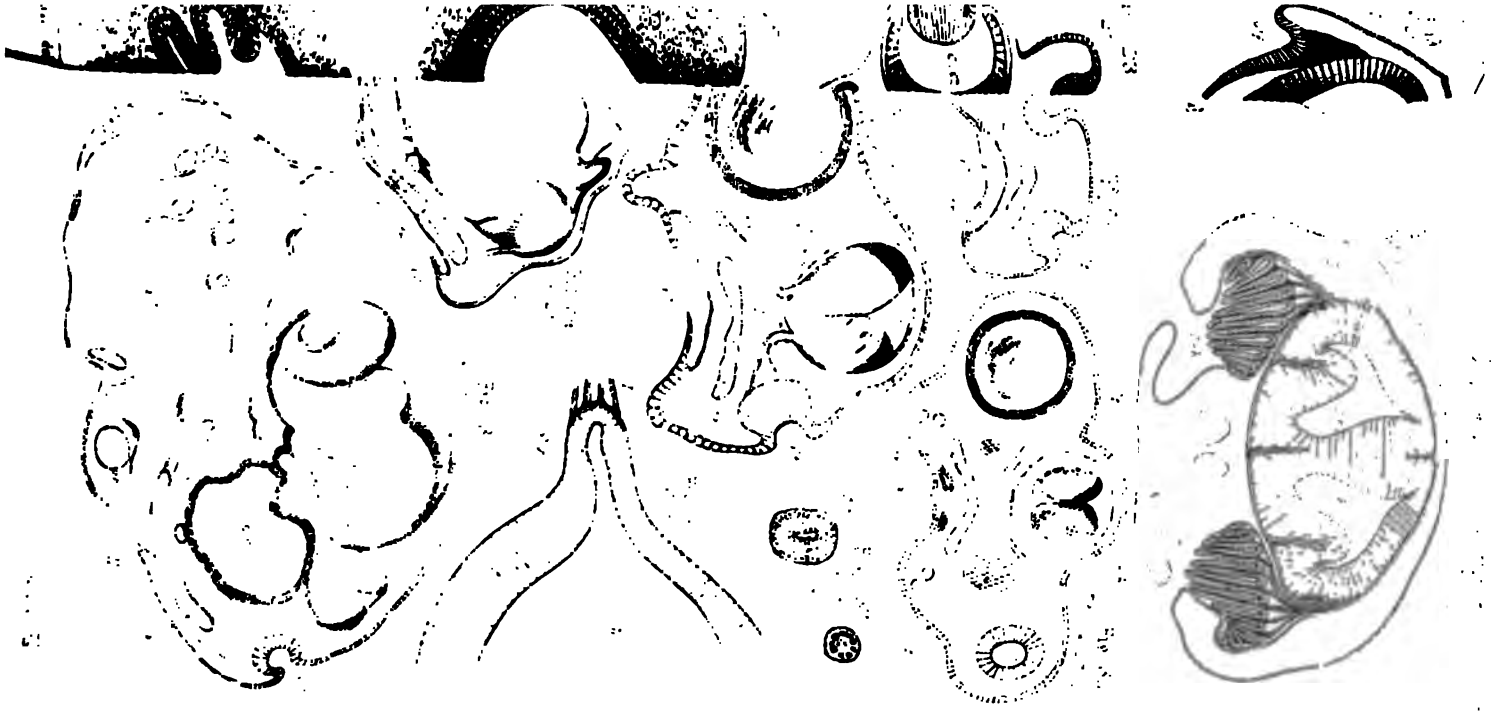
FIG. 3.—Longitudinal and vertical section through the head of a sixty-seven hours' chick embryo, showing the olfactory pit, the maxillary, mandibular, hyoidean, and first three branchial arches, with the intervening clefts. Picric acid. × 20 diam.

FIGS. 4—6.—Longitudinal and vertical sections through the head of a ninety-six hours' chick. Picric acid. × 15 diam.

FIG. 4.—The most superficial of the series; shows the maxillary, mandibular and hyoidean arches, with their intervening clefts, and the trigeminal, facial, and auditory nerves.







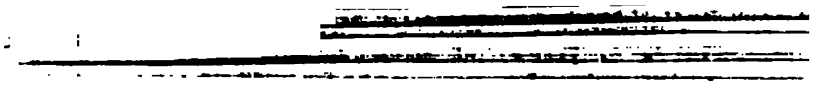


FIG. 5 shows, in addition, the olfactory pit and the distal end of the olfactory nerve.

FIG. 6 shows the third, glossopharyngeal and vagus nerves.

FIGS. 7 and 8.—Longitudinal and vertical sections through the cerebral hemispheres and nasal region of a six-day chick embryo. Picric acid. × 15 diam.

FIG. 7 shows whole length of olfactory nerve.

FIG. 8 shows ganglion at root of origin of olfactory nerve, also internal projection of hemisphere at this point.

FIG. 9.—Longitudinal and vertical section through the nasal region of a seven-day chick embryo, showing whole length of olfactory nerve, and commencing rudiment of olfactory lobe. Picric acid. × 15 diam.

FIG. 10.—About half of a transverse section through the forebrain of a four-day duck embryo, showing the olfactory nerve and pit. Picric acid. × 56 diam.

FIGS. 11 and 12.—Tranverse sections through the anterior part of the head of an eighty-hours' chick embryo, passing through the cerebral hemispheres, and the olfactory pits and nerves. Picric acid. × 27 diam.

FIG. 11 shows on left side the origin of the olfactory nerve.

FIG. 12 shows on right side the distal end of the olfactory nerve.

FIG. 13.—Longitudinal and horizontal section through the head of a dogfish embryo of stage K, showing early stage in development of the olfactory pits. Chromic and osmic acids. × 20 diam.

FIG. 14.—Transverse section through the anterior extremity of the head of a dogfish embryo of stage K, showing the forebrain, the olfactory pits and nerves. Chromic and osmic acids. × 20 diam.

FIG. 15.—Longitudinal and vertical section through the head of a dogfish embryo of stage M, showing the olfactory pit and nerve. Chromic and osmic acids. × 20 diam.

FIG. 16.—Longitudinal and vertical section through the head of a dogfish embryo of stage M, showing the olfactory pit, the mandibular, hyoid and branchial arches. Chromic and osmic acids. × 20 diam.

FIGS. 17 and 18.—Longitudinal and vertical sections through the head of a dogfish embryo of stage O. Chromic and osmic acids. × 20 diam.

FIG. 17 shows olfactory pit and nerve.

FIG. 18 shows olfactory pit, with Schneiderian fold, olfactory nerve, forebrain, hyoid and branchial arches.

FIG. 19.—Transverse section through the forebrain of a dogfish embryo of stage M, showing olfactory pits and nerves, with absence of olfactory lobes. Chromic and osmic acids. × 27 diam.

FIG. 20.—Transverse section through the same region as in the preceding figure, but in a dogfish embryo at the commencement of stage O: shows olfactory pits with Schneiderian folds, olfactory nerve, and commencing olfactory lobe. Chromic and osmic acids. × 27 diam.

FIG. 21.—Transverse section through the forepart of the head of a dogfish embryo at a stage intermediate between O and P, showing the forebrain, the olfactory pits, and on the left side the olfactory nerve and olfactory lobe. × 17 diam.

FIG. 22.—Transverse section through the forepart of the head of a dogfish embryo of stage Q, showing the cerebral hemispheres, olfactory lobes, olfactory nerves, and olfactory pits with their Schneiderian folds. × 9 diam.

FIGS. 23—26.—Sections through a dogfish embryo of stage N, showing the resemblances between the gills and the Schneiderian folds. Chromic and osmic acids.

EXPLANATION OF PLATES XIII, XIV—*Continued.*

FIG. 23.—Longitudinal and horizontal section through the head, showing fore- and hindbrain, third and trigeminal nerves, eyes and olfactory pits. × 20 diam.

FIG. 24.—Transverse section through forepart of body, showing spinal cord, with anterior and posterior roots of a spinal nerve, vagus nerve, cardiac and dorsal aorta, branchial arteries, pharynx and gills. × 20 diam.

FIG. 25.—The right olfactory organ from the same section as fig. 23 more highly magnified, showing the characters of the Schneiderian folds. × 90 diam.

FIG. 26.—The left gill from fig. 24 more highly magnified, showing histological characters of the gill folds. × 90 diam.

FIGS. 27 and 28.—Sections from a dogfish embryo about stage o, showing resemblance between gills and Schneiderian folds at a rather later period. × 90 diam.

FIG. 27.—Through Schneiderian folds.

FIG. 28.—Through gill.

FIG. 29.—Transverse section through the anterior extremity of the head of a trout embryo on the twenty-seventh day after fertilisation of the ova, showing forebrain, olfactory pits, and on the left side the olfactory nerve. Picric acid. × 56 diam.

FIG. 30.—Longitudinal and vertical section through the head of a trout embryo on the thirtieth day, showing mid- and hindbrains, roots of visceral arches and clefts, and the olfactory pit. Picric acid. × 56 diam.

FIG. 31.—Transverse section through the anterior extremity of the head of a salmon embryo about the time of hatching, showing olfactory pits, trabecular plate, and anterior prolongations of the buccal cavity. Chromic and osmic acids. × 27 diam.

FIG. 32.—Transverse section through the forepart of the head of a salmon embryo about a week after hatching, showing forebrain, eyes, olfactory pits, and paired-anterior diverticula of the buccal cavity. Picric acid. × 27 diam.

FIG. 33.—Transverse section through the forepart of the head of a salmon embryo two days after hatching, showing forebrain, and on the left side the eye, on the right the olfactory nerve and organ. Chromic and osmic acids. × 35 diam.

FIGS. 34 and 35.—Longitudinal and vertical sections through the head of a salmon embryo of the same age as that in the preceding figure. Chromic and osmic acids. × 27 diam.

FIG. 34.—Section taken close to median line, showing root of olfactory nerve, optic nerves, infundibulum, and anterior prolongation of buccal cavity.

FIG. 35.—More superficial section, showing olfactory pit, eye, pharynx with its branchial arches, and the anterior prolongation of the buccal cavity.

FIG. 36.—Longitudinal and vertical section through the forepart of the cerebral hemisphere, the olfactory lobe and olfactory nerve of a twelve-day chick embryo. Picric acid. × 17 diam.

FIGS. 37, 39.—Transverse sections through same region as preceding figure in a twelve-day chick embryo. Picric acid. × 17 diam.

FIG. 37.—Through the olfactory nerve.

FIG. 38.—Through the olfactory lobe.

FIG. 39.—Through the anterior part of the cerebral hemisphere.

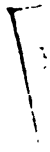


Fig. 1.

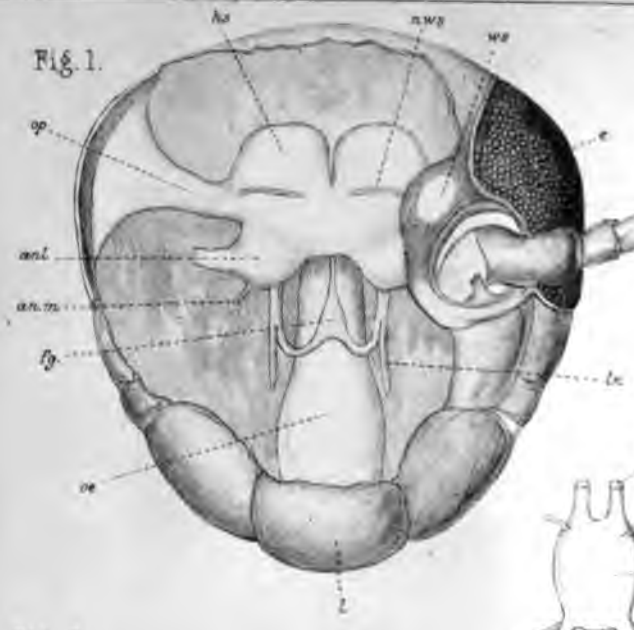
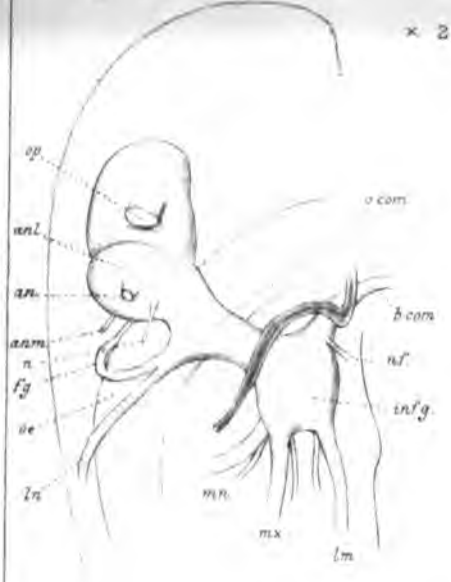
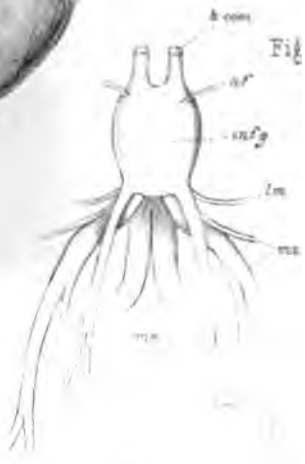


Fig. 2.





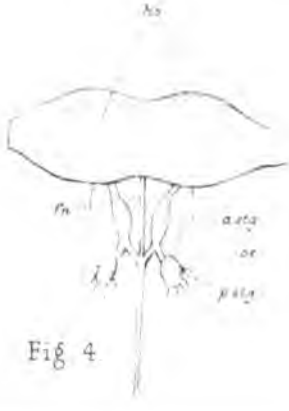


Fig 4

E T E. ad nat. del.
F. Huth Lith.

Fig. 5. × 60
ecx
cau
gc
gc
gc
anl
Fig. 6. × 60
icx
cau
gc
op
gc
an
t
Fig. 7. × 60
exc
ocx
icx
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a.com
ann
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Fig.
250
gc
c
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Fig. 13. × 250
ocx
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icx
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Fig. 15.

EXPLANATION OF PLATES XV, XVI.

Illustrating Mr. E. T. Newton's paper on the Brain of the Cockroach, *Blatta orientalis*.

All the figures, except Nos. 3 and 4, drawn with camera lucida.

REFERENCES.

hs. Hemisphere of brain. *e.* Facetted eye. *ant.* Antenna. *an.* Antennary nerve. *l.* Labrum. *ws.* White spot. *nws.* Nerve to white spot. *op.* Optic nerve or ganglion. *anl.* Antennary lobe. *nms.* Nerve to antennary muscle. *fg.* Frontal ganglion. *ln.* Nerve to labrum. *oe.* Œsophagus. *mn.* Nerves to mandible. *mx.* Nerves to maxillæ. *lm.* Nerves to labium. *inf. g.* Infra-œsophageal ganglion. *o. com.* Œsophageal commissure. *b. com.* Commissure to body ganglion. *nf.* Nerve to muscles (?) near foramen magnum. *a. stg.* Anterior stomato-gastric ganglion. *p. stg.* Posterior stomato-gastric ganglion. *fn.* Median nerve from frontal ganglion. *a. com.* Antennary commissure. *t.* Trabecula. *p.* Peduncle. *icx.* Inner calix of corpus fungiforme. *ocx.* Outer calix of corpus fungiforme. *cxc.* Cells of calix. *c.* Corpus centrale. *cau.* Cauliculus. *gc.* Ganglionic cells. *nfg.* Nerve from œsophageal commissure to frontal ganglion and labrum. *n.* Nerve from back part of antennary lobe.

PLATE XV.

FIG. 1. –Front view of head. × 25 diameters. Chitin partly removed to show position of brain and general relation of parts.

FIG. 2.—Side view of brain, with infra-œsophageal ganglion. × 25 diam.

FIG. 3.—Infra-œsophageal ganglion, seen from behind, with nerves to the mouth organs. × 25 diam.

FIG. 4.—The brain and stomato-gastric ganglia seen from above. The latter resting on œsophagus. × 25 diam.

PLATE XVI.

FIGS. 5 to 10.—Frontal sections of brain, selected from a series of 34 made from one specimen. × 60 diam. Fig. 13 represents the entire section; in the others only one half is drawn.

FIG. 5.—Section No. 2 from front, showing the *cauliculus* covered by the cells of the *calices*.

EXPLANATION OF PLATE XVI—*Continued.*

FIG. 6.—Section 6, shows *cauliculus*, *trabecula*, the commencement of the *peduncle*, portions of the *calices* and their cells, &c.

FIG. 7.—Section 10, shows the *cauliculus* becoming reduced in size, the *peduncle* increasing, and the *calices* becoming deeper.

FIG. 8.—Section 13, shows the *cauliculi* almost obsolete, the *peduncle* on each side joining the outer *calix*, and the *calices* very deeply curved.

FIG. 9.—Section 20. The *peduncle* is lost as well as the *cauliculus*, and the *trabecula* is much smaller.

FIG. 10.—Section 24. A portion of only one *calix* is seen. The *trabecula* still remains.

FIG. 11.—*Corpus centrale* from section 14, for comparison with the same structure in Sections 13 and 20.

FIG. 12.—A portion of a *calix* (*ex.*) from Section 15, to show the calicular cells and fibres. × 250 diam.

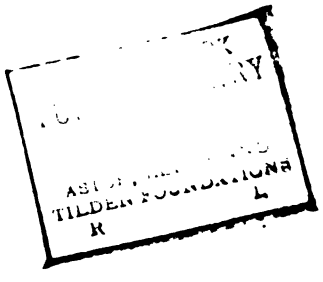
FIG. 13.—Ganglionic cells from Section 24, showing the granular contents passing into the fibres. × 250 diam.

FIG. 14.—Small portion of network of fibres from the lower part of *peduncle*. × 620 diam. In the upper part of *peduncle* the meshes become more elongated, in the *trabeculæ* and *cauliculus* they are less elongated and more regular.

FIG. 15.—View, from the inner side, of the *trabecula*, *cauliculus*, *peduncle*, and *calices* of the right side of the brain, separated from all the surrounding parts. This figure is taken from the model mentioned in the text (p. 350).

FIG. 16.—Ditto, seen from above.

FIG. 17.—Ditto, seen from the front.


TILDEN FOUNDATIONS

DESCRIPTION OF PLATE XVII,

Illustrating Surgeon T. R. Lewis's paper on the "Microphytes of the Blood." The developmental stages of Organisms found in the Blood of Healthy Animals shortly after death.

FIG. 1.—A tracing of bacilli from a micro-photograph. Magnified 1100 diameters.

FIG. 2.—Growth of ditto into long filaments. Magnified 600 diameters.

FIG. 3.—Formation of 'spores' in ditto.

FIG. 4.—The filaments having become nearly invisible, the 'spores' only are seen, arranged linearly. Magnified 600 diameters.

FIG. 5.—Isolated 'spores' in the condition sometimes described as "germinating." Magnified 1000 diameters (fig. *a*, *b*, magnified 2000 diameters).

FIG. 6—8.—The developmental stages of a bacillus *below* the average dimensions. Magnified 1000 diameters.

FIG. 9.—Bacilli *above* the average dimensions. One white and two red blood-corpuscles are outlined in the figure. Magnified 1000 diameters.

FIG. 10.—Ditto, showing growth into filaments. Magnified 1000 diameters.

FIG. 11.—Ditto, subsequently undergoing fission. Magnified 1000 diameters.

FIG. 12.—Spore-like bodies which formed in a portion of the filaments delineated at fig. 10. Magnified 1000 diameters.

EXPLANATION OF PLATE XVIII,

Illustrating Dr. Klein's Memoir on the "Glandular Epithelium and Division of Nuclei in the Skin of Newt."

Fig. 1.—Part of a large saccular gland of tail of newt. *a*, epithelial cells (**nearest the** duct) filled with fat globules; *b*, epithelial cells, one part **of which** contains large, highly refractive granules; *c*, cells indicated **merely in** outline. Drawn on Crouch's small stand, with his $\frac{1}{8}$ obj.

Figs. 2, 3, 4, 5, 6, and 7 represent giant nuclei of the epithelial cells lining **the above** glands, examined fresh on the warm stage on Crouch's **small stand with Zeiss's E obj.**

Figs. 4 and 7 represent nuclei in the stage of division.

Figs. 8—35 are nuclei of the deep layer of (columnar) epithelial cells of the epidermis of the tail of newt.

Figs. 8—35 and Fig. 33 show the outlines only of the respective epithelial cells.

Figs. 8 and 9 represent ripe nuclei, *i. e.* nuclei possessed of a limiting membrane, a uniform dense network with dots (fibrils viewed in section), and a pale, transparent interstitial substance.

Figs. 10, 11, 12, and 13 represent nuclei, in which the fibrils of the intra-nuclear network become twisted and convoluted, and arranged more or less in the shape of a 'basket.' The nuclear membrane has become indistinct.

Figs. 14, 15, 16, 17, 18, and 19 represent nuclei, in which the fibrils have become so arranged that they are radiating towards the centre, 'wreath,' and single star, monaster. A nuclear membrane is not present.

Figs. 20, 21, and 22 show nuclei, in which the network of fibrils has become arranged as a double star, dyaster. The nuclear membrane is not present.

Figs. 23, 24, and 25 show daughter nuclei, *i. e.* after the mother nucleus has divided.

Figs. 8—15 and 18—25 drawn with Zeiss's E.

Figs. 16 and 17 with Zeiss's oil immersion, $\frac{1}{18}$ obj.

Figs. 26—32 show nuclei, dividing by simple cleavage.

Figs. 33—35 show dividing nuclei, in which the network had arranged itself as in the former cases when nuclei are going to divide after the indirect fashion; but the division is, after all, after the direct manner of cleavage.

Figs. 26—35 drawn with Zeiss's E obj.

Fig. 1.

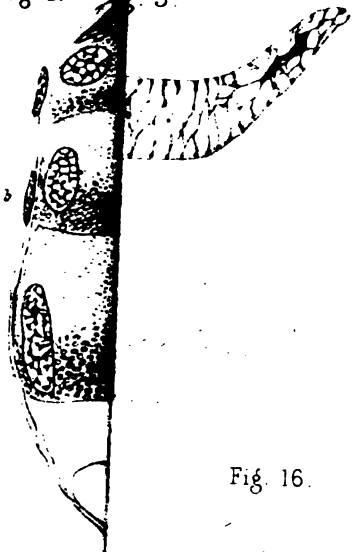


Fig. 3.

Fig. 4

Fig. 26.

Fig 27.

Fig. 16.

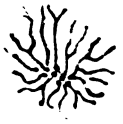


Fig. 28.

Fig 29.

Fig. 8.

Fig. 17.

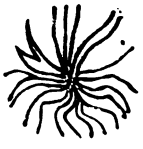


Fig 30.

Fig 31.

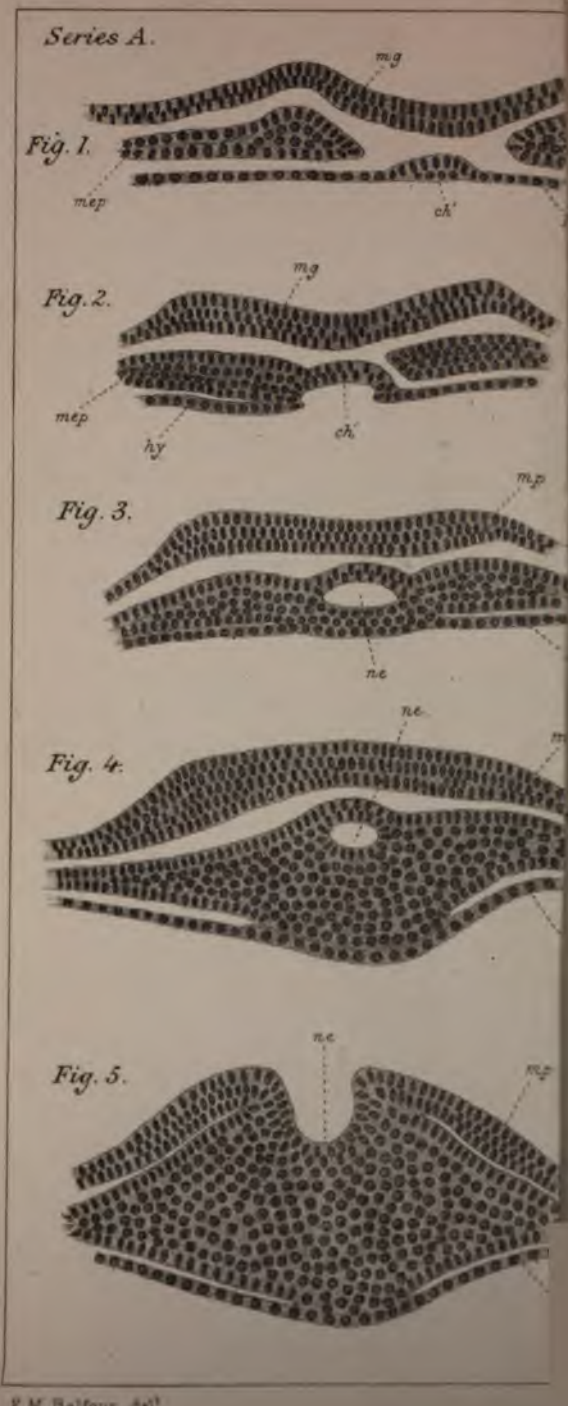
Fig. 32

Fig. 33.

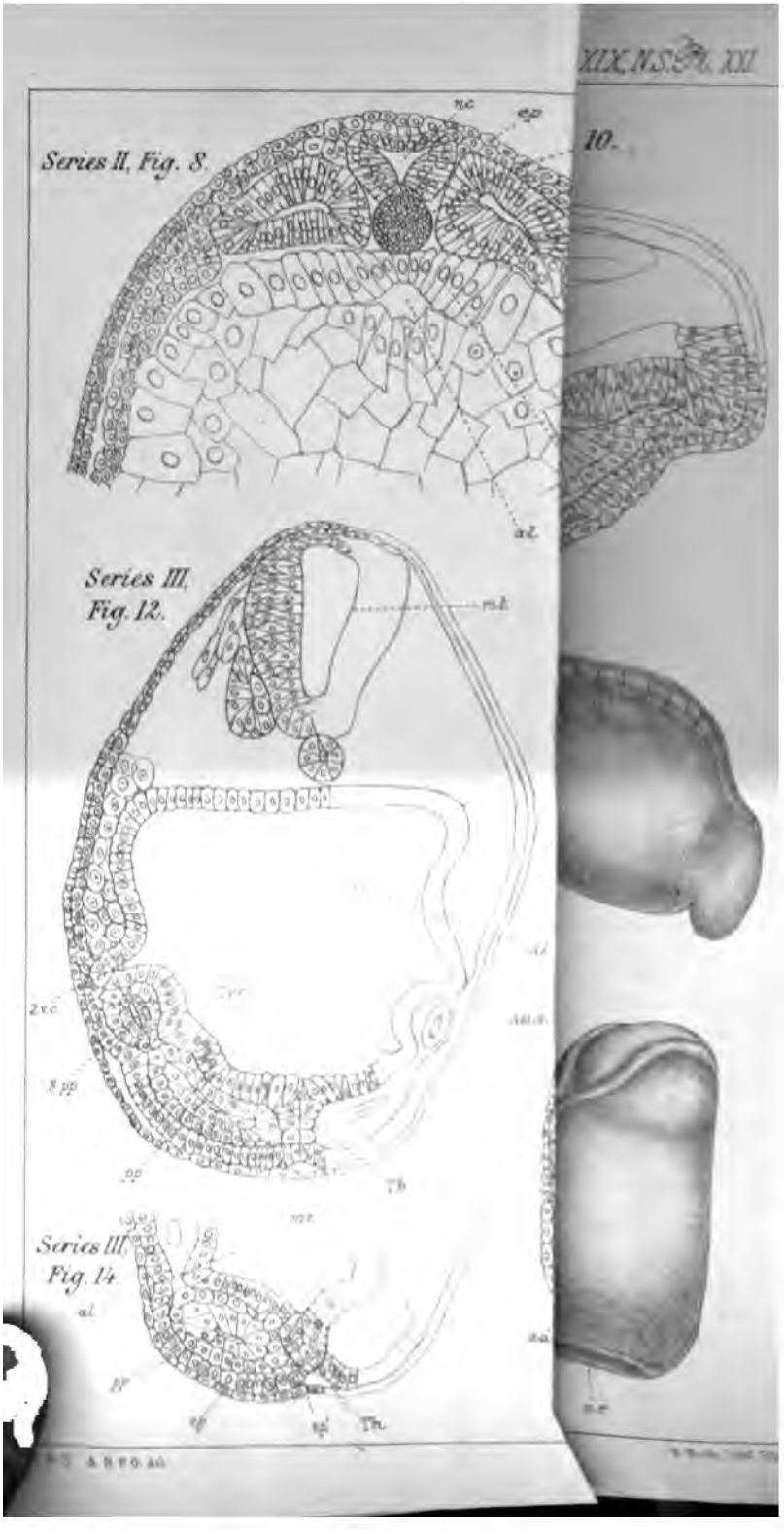
Fig. 34

Fig. 35

Fig. 36



F. M. Balfour, del.


Series II, Fig. 8.
nc
ep
al
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Series III.
Fig. 12.
md
2vc
spp
pp
Th
Series III.
Fig. 14
al
pp
ep
ep'
Th.

EXPLANATION OF PLATES XX AND XXI.

Illustrating the Memoir on some Points in the Early Development of the Common Newt (*Triton tæniatus*), by W. B. Scott, B.A., and Henry F. Osborn, B.A.

With the exception of fig. 1 the following figures were drawn with a Zeiss' A objective. In figs. 2, 3, 4, 5, a No. 2 (Zeiss) eyepiece was used, and for figs. 6 and 7 a No. 3 eyepiece.

EXPLANATION OF PLATE XX.

LIST OF REFERENCES.

ep. Epiblast. *ep'.* Inner layer of epiblast. *yk.* Yolk. *hy.* Hypoblast. *in. hy.* Invagination hypoblast. *y. hy.* Yolk hypoblast. *m.* Mesoblast. *sp.* Splanchnopleure. *so.* Somatopleure. *al.* Alimentary canal. *nc.* Neural canal. *ch.* Notochord. *mg.* Medullary groove. *mf.* Medullary folds.

FIG. 1.—Longitudinal section of an embryo at time of commencement of invagination. Hartnack No. 7 obj., eyepiece 3. It shows one of the earliest stages of the epiblast.

FIG. 2.—Represents a longitudinal section of a Triton embryo (probably *cristatus*) in the early part of Stage A. At the opening of the blastopore the section is in the median line. It slants off forwards, however, to one side, and therefore out of the region of the alimentary canal. It shows the formation of the invagination-hypoblast and the confused mass of cells arising from the reflection of the epiblast.

FIG. 3.—A section of the same embryo. It may be considered the reverse of the last. At the blastopore it is at one side of the median line, while anteriorly it is directly in the median line. This obliquity explains the apparent upgrowth of yolk-cells in the centre. Putting this and the previous section together, a fair idea may be obtained of the actual relation of the layers at this period. It illustrates the formation of mesoblast by invagination, and the obliteration of the segmentation cavity by the advance of the alimentary canal. The blastopore has been artificially widened.

FIG. 4.—An anterior transverse section of an embryo, at Stage A, slightly more advanced than the previous one. It shows the shallow medull groove, the lateral plates of mesoblast extending half way down the

EXPLANATION OF PLATE XX—*Continued.*

also the invagination-hypoblast above the alimentary canal continuous at the sides with the yolk hypoblast.

FIG. 5.—A transverse section through the head region of an embryo of Stage B. It shows the splitting of the mesoblast and the formation of the medullary plate and notochord.

FIG. 6.—A transverse section through the trunk region of an embryo at Stage C, showing a slightly more advanced development than the last.

FIG. 7.—Represents a transverse section through the anterior trunk region late in Stage D.

EXPLANATION OF PLATE XXI.

LIST OF REFERENCES.

op. Optic vesicle. *pp.* Head cavities (numbered in order 1, 2, &c.) *vc.* Visceral clefts. *aa.* Aortic arches and auditory vesicles. *eb.* External branchia. *mb.* Mid brain. *hb.* Hind brain. *th.* Thyroid body. *al.* Alimentary canal. *ep.* Outer layer of epiblast. *ep'.* Inner layer of ditto. Zeiss. A, obj. cc. No. 2, except for figs. 9, 16, and 17.

FIG. 8.—Another transverse section in the middle region. This section is cut obliquely, so that the lateral and vertebral plates of mesoblast do not appear continuous with the mesoblast lining the sides of the embryo; it gives therefore at first sight a false impression.

FIG. 9.—Enlarged view of the lateral epiblast of fig. 6. Zeiss D, ocul. 3. *a.* One point of cell division.

FIG. 10.—Horizontal longitudinal section through the head of an embryo of Stage F. The section is slightly oblique, and hence unsymmetrical. It shows the unsegmented head cavity.

FIG. 11.—Vertical longitudinal section through the head of an embryo of Stage K, showing the relations of the head cavities, aortic arches, and gill clefts; it is taken too much at the side to show the thyroid.

FIG. 12.—Transverse section through head of an embryo of Stage I.

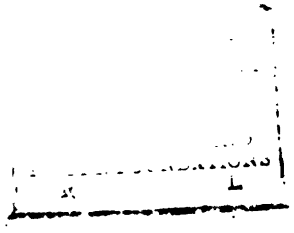
FIG. 13.—Transverse section of head of embryo very slightly older than the preceding figure.

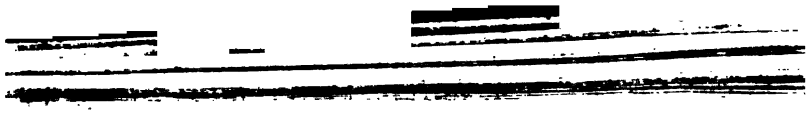
FIG. 14.—Section through the same embryo as fig. 12, but considerably further forwards.

FIG. 15.—Transverse section through the head of an embryo of about Stage M.

FIG. 16.—External drawing of an embryo of Stage D. *s. r.* Sinus rhomboidalis.

FIG. 17.—External drawing of an embryo of Stage I. *o.* Oral involution.





DESCRIPTION OF PLATE XXII,

Illustrating Professor Ray Lankester's Memoir "On the Structure of Haliphysema."

FIG. 1.—*Haliphysema Tumanowiczii*, Bowerbank, drawn from a specimen, placed while living in weak chromic acid ($\frac{1}{4}$th per cent.), and subsequently preserved in strong alcohol. *pl.* Streaming protoplasm investing the spicula. *esp.* Spicules derived from Esperia. *ren.* Spicules derived from Reniera.

FIG. 2.—Protoplasmic core of a similar specimen, obtained by gently crushing the test. The core as drawn is a restoration of a specimen broken into three pieces. It is somewhat *flattened*, and therefore widened by pressure. Anteriorly the egg-like bodies are seen embedded in the solid protoplasm. The surface of the core is grooved or ribbed by the longitudinally placed spicules forming the test.

N.B.—Figs. 1 and 2 are magnified 135 times linear.

FIG. 3.—A spicule of the test (derived from a Reniera) showing investment of streaming protoplasm. *n.* One of the vesicular nuclei. From a specimen preserved in chromic acid followed by alcohol.

FIG. 4.—Egg-like body; from a similarly preserved specimen teazed.

FIG. 5.—Vacuolated protoplasm and large and small corpuscles; from a similar specimen.

FIG. 6.—Egg-like bodies from a similar specimen; one is in the process of transverse fission.

FIG. 7.—Portion of the protoplasm showing the wall of cavities in which egg-like bodies were embedded.

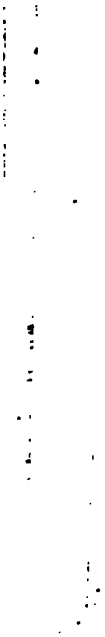
FIG. 8.—Corpuscle similar to those of fig. 5.

FIG. 9.—Vacuolated, reticular protoplasm, with a number of the characteristic vesicular nuclei embedded. From a chromic-acid-alcohol specimen, teazed.

FIG. 10.—Vesicular nuclei of Haliphysema, showing various forms of collapse due to the action of reagents. *a*, *b*. Still spherical. *c*. Invaginated hemisphere. *d*. False appearance of transverse septum and fission. *e*. Lateral view of *d*.

FIG, 11.—Portion of the core of a specimen hardened in $\frac{1}{4}$ per cent. chromic acid, followed by alcohol, then stained with hæmatoxylin, mounted in oil of cloves and Canada balsam, and carefully crushed whilst in the last-named medium. The vesicular nuclei, darkly stained, are seen besides smaller corpuscles. *c*. Cavity from which a vesicular nucleus has been removed. *r*. Ridges fitting into the interstices of the test.

N.B.—Figs. 3 to 11 represent the objects of 280 times the natural size, linear.



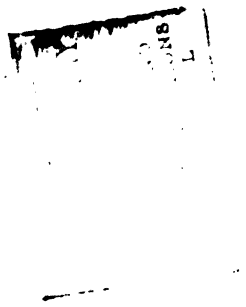


Fig. 1.

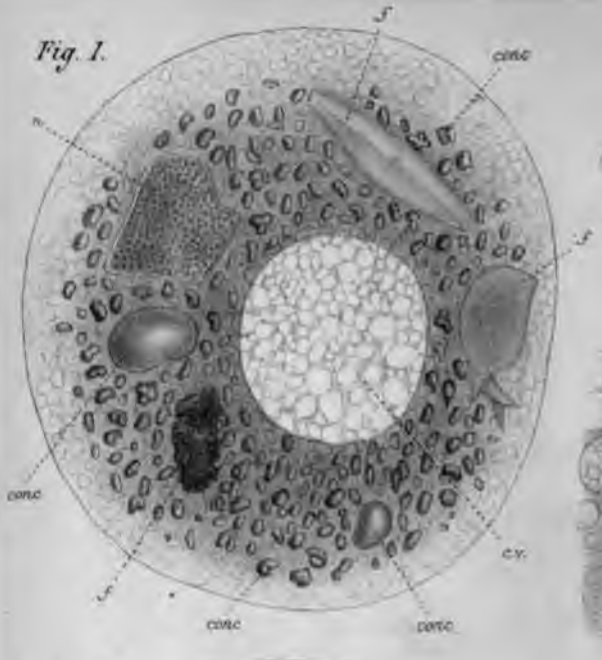


Fig. 3.

Fig. 4.

Fig. 2.

Fig. 5.

Fig. 7.

Fig. 6

Fig. 8.

LITHAMŒBA.

EXPLANATION OF PLATE XXIII,

Illustrating Professor Ray Lankester's "Description of *Lithamœba discus*, nov. gen. et sp., one of the Gymnomyxa."

FIG 1.—*Lithamœba discus* at rest; magnified about 350 dinmeters. *n.* nucleus; *conc.* concretions; *f.* food matters; *cv.* contractile vacuole.

FIG. 2.—The same specimen actively extruding pseudopodia.

FIG. 3.—Another specimen (less magnified) killed by iodine solution.

FIG. 4.—The vacuolar structure of the protoplasm, as seen under No. 10 immersion lens, in a specimen treated with osmic acid and picro-carmine.

FIG. 5.—The angular nucleus and its investing membrane after the action of dilute acetic acid.

FIG. 6.—The granular cuticle in optical section, after the action of iodine solution.

FIG. 7.—The granular cuticle, surface view, after the action of iodine solution.

FIG. 8.—A concretion isolated.

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DESCRIPTION OF PLATE XXIV,

Illustrating Mr. Gibbes' Memoir on the "Structure of the Vertebrate Spermatozoon."

FIG. 1.—*S. maculata.* Fresh. Drawn with Powell and Lealand's $\frac{1}{16}$ imm. × 950.

FIG. 2.—*S. maculata.* Fresh. Drawn with Powell and Lealand's $\frac{1}{8}$ new formula imm.; upper part of filament was in motion at the time.

FIG. 3.—*Triton cristatus.* Prepared in 5 per cent. chronic ammonium, and mounted in glycerin. Drawn with Ziess' F.

FIG. 4.—Spermatozoon of horse, fresh mounted in glycerin. Drawn with Powell and Laland's $\frac{1}{16}$ immersion. × 950.

FIG. 5.—Spermatozoon of guinea-pig, fresh mounted in glycerin. Drawn with $\frac{1}{16}$ immersion. × 950.

FIG. 6.—Spermatozoon of *Salamandra maculata*, mounted in a solution of chloride of sodium $\frac{1}{2}$ per cent., and drawn, after having been mounted forty-eight hours, with Zeiss' F.

FIG. 7.—Spermatozoon of *Triton cristatus*, taken fresh and mounted in $\frac{1}{2}$ per cent. solution of chloride of sodium, and drawn with Powell and Lealand's $\frac{1}{16}$ dry, after being mounted four weeks.

FIGS. 8 and 9.—Spermatozoon of *S. maculata*, taken fresh and mounted in $\frac{1}{2}$ per cent. salt solution. Drawn with Powell and Lealand's $\frac{1}{8}$ immersion. In Fig. 8 the head and membrane have altogether disappeared, while in Fig. 9 they are scarcely touched.

FIG. 10.—Spermatozoon of *S. maculata* after immersion in a 5 per cent. solution of Sodæ Bicarb. for forty-eight hours. Drawn with $\frac{1}{16}$ of immersion.

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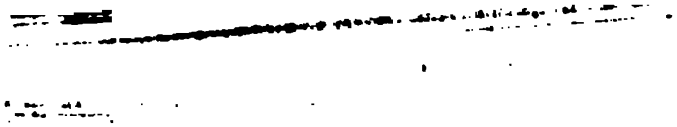
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